THE EARLIEST GOATS AND OTHER ANTELOPES FROM THE SAMOS *HIPPARION* FAUNA

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SYNOPSIS

Lower Pliocene antelopes belonging to *Palaeoryx*, *Protoryx* and *Pachytragus* and hitherto taken as Hippotragini, are revised and placed in the Caprinae. The species of *Protragelaphus*, *Prostrepsiceros* and *Palaeoreas* are likewise revised; the last two genera have normally been classified as Tragelaphini, but *Prostrepsiceros* should join *Protragelaphus* in the Antilopini and *Palaeoreas* is in the Ovibovini. Hippotragini and Tragelaphini are almost totally African, Caprinae and Ovibovini almost all Eurasian, and those Antilopini to which *Prostrepsiceros* and *Protragelaphus* are related are also Eurasian. Thus the Samos fossil fauna contains no antelopes related to living African species; it is more properly seen as a stage in the evolution of Eurasian bovid faunas.

I. INTRODUCTION

Towards the end of the nineteenth century Major (1888, 1891a, 1891b, 1894) collected fossil mammals on the Aegean island of Samos very close to the mainland of Turkey, and recognized a later Tertiary fauna similar to that already known from Pikermi in Attica. Much of his collection passed to the Geology Department of Lausanne University, some was purchased by the British Museum (Natural History) in 1889 and 1890, and more pieces went to other museums. Before the First World War collectors provided material for geological institutes in Munich, Münster in Westphalia and Stuttgart, and for the museum in Vienna, and in 1924 Brown collected for the American Museum of Natural History, New York. His field notebook contains meagre details of the quarries which he excavated, and their positions were shown on a small map in Brown (1927 : 19). Quarry 1 was in the Adriano district on land owned by the Soufoulis family; this quarry was near former German excavations and about 1½ miles north of Mytlini; quarry 2 was in the Potamies district on land owned by Trifon Balidakis; quarry 3 was in the Megalosvrakos district on land owned by Trifon Balidakis, but no Bovidae are known from this quarry; quarry 4 was in the Potamies district on land owned by Dr Gliarmis; quarry 5 was in the Limitzis district on land owned by the widow Soumena; quarry 6 was in the Tholoramo or Vigles district on waste land.

Despite all this collecting, there is little information on the geology of the fossiliferous deposits. Stefani (*in* Stefani, Major and Barbey, 1892) acknowledged accounts of some earlier travellers, and noted two basins of Tertiary lacustrine or marshy deposits, that of Mytilini occupying a large part of the island east of Ambelos, and that of Karlovassi farther west. Brown (1927) gave a summary of the deposits. Schlosser (1904 : 112) noted from the matrix on the fossils that different associations of bovid species occurred in different compositions of the sediments. Abel (1922 : 143) considered that the Samos fauna had been catastrophically annihilated in volcanic eruptions, but that the absence of associations of the skeletal parts indicated postmortem stream transport.

J. A. Van Couvering (pers. comm.) writes as follows. 'Tertiary sediments of the Mytilini district consist of well-bedded volcanic sediments—siltstones, sandstones, and volcanic pebble breccias—interlayered with freshwater algal limestones and marble cobble conglomerates (Van Couvering & Miller, 1970). The only authigenic minerals within the sequence are calcite (in the limestones and locally as cement in the sediments) and silica, which appears only in a thin-layered cherty limestone formation near the top of the sequence. No soil horizons appear to have been developed in the sequence, and no angular unconformities can be detected, indicating that deposition was more or less continuous. The sequence is one which seems most likely to have developed in a slowly subsiding intermontane basin surrounded by upfaulted marble basement and traversed by low-gradient streams carrying mostly fine-grained volcanic detritus from the nearby active Cappadocian pyroclastic province to the east (Westerveld 1957). The basin floor was periodically submerged in shallow lakes, probably after activity on the faults to the west and northeast which now show downthrow towards the basin, and the water in the lakes and in the subsurface was high in dissolved carbonate from the basement. The zeolites and authigenic feldspar which might have formed in a more arid, alkaline environment from the volcanic detritus (Hay 1966) are absent, which suggests that the steppe climate of the Samos fauna was more like that of the temperate zone grasslands than the African savannah. The fossils occur in a variety of volcanic sediment types (Schlosser 1904) in the main horizon at Adrianó (Soufoulis farm), but not in association with primary ash falls accounting for the deaths of the animals. Suggestions that the algal limestones formed in a Pontian "Aegan lake" (Spratt 1846) or that the alluvial beds are part of the valley fill in an ancient course of the Maeander or Menderes River (Brown 1927) are unsupported by the geological evidence.'

A group of antelopes which is more abundant at Samos than at any other site is that of *Palaeoryx* and *Pachytragus*, and I shall here reconsider their classification. A second group in the Samos fauna which will be similarly treated contains the spiral-horned *Protragelaphus*, *Prostrepsiceros* and *Palaeoreas*. Two other lower Pliocene sites broadly contemporaneous with Samos will be referred to, those of Maragha in northern Persia (see Pohlig 1886 and Mecquenem 1908) and Pikermi in Greece (Woodward 1901). Pikermi has material of *Protoryx*, a relative of *Palaeoryx* and *Pachytragus*, and Maragha has a diversity of spiral-horned antelopes. However, it is the presence of so many complete skulls, crania and dentitions of bovids and the large number of species in the Samos deposits, which give that fauna its decisive importance. Adequate discussion of these antelopes involves referring to other fossil genera, and necessitates giving opinions about their classification. Nevertheless my revision covers only species of the above six genera occurring at Samos, Pikermi and Maragha. During this study I have had access to previously published material in European museums and to unpublished material in New York. The initials BM(NH) indicate material in the British Museum (Natural History) in London, and AMNH in the American Museum of Natural History, New York. Measurements are always expressed in millimetres.

II. SYSTEMATICS OF *PALAEORYX*, *PROTORYX* AND *PACHYTRAGUS*

The first of the *Palaeoryx* group to be discovered was the large *Antilope pallasi* Wagner (1857 : 149) from Pikermi, of which the type specimen is still in Munich. Gaudry founded the generic name *Palaeoryx* for this species although he actually intended the name as a subgenus. He likened the fossil particularly to *Oryx* among living antelopes and since then it has always been considered a member of the Hippotragini. Schlosser (1904 : 38 and 43) added two more species from Samos, *P. majori* and *P. ingens*, the latter based only on teeth, and Andree (1926 : 161) added *P. laticeps*. Some other species formerly supposed to belong to *Palaeoryx*, particularly the fine later Pliocene skulls of '*Palaeoryx*' *boodon* and '*Palaeoryx*' *cordieri* in Paris have been placed in a separate boselaphine or bovine genus *Parabos* by Arambourg and Piveteau (1929a : 144), and others may belong to *Leptobos* (Pilgrim and Hopwood 1928 : 74).

Major (1891a : 608–609) founded the genus *Protoryx* for some antelopes from Samos similar to *Palaeoryx*, but having more compressed horn cores and sometimes a longer cranium. He considered *Protoryx* to have more striking resemblances to Hippotragini than did *Palaeoryx*. He referred to the new genus a Pikermi cranium figured but not named by Gaudry (1865 : 289, pl. 52 fig. 1 'Antilope d'espèce indéterminée') and a skull from Maragha, BM(NH) M.3841 which was not figured. Four species were named as occurring at Samos, *P. carolinae*, *P. longiceps*, *P. gaudryi* and *P. hippolyte*, none of which were given diagnoses or figures. *P. carolinae* is the only one he cited as occurring at Pikermi, and for this reason Pilgrim and Hopwood (1928) later selected *P. carolinae* as the name for Gaudry's illustrated cranium.

Schlosser (1904 : 45) corrected the generic diagnosis in which Major had mistakenly referred to the braincase being very little angled on the face, referred three Samos skulls to *P. carolinae* Major (Schlosser 1904 : 45, pl. 9 figs 1, 4, 8) and a frontlet to *P.* cf. *carolinae*, founded a second species *P. hentscheli* on teeth only, and suggested that another new genus and species of his, *Pseudotragus capricornis*, might include material of Major's *nomina nuda Protoryx gaudryi* and *P. hippolyte*. He founded a new genus and species *Pachytragus crassicornis* differing from *Protoryx* by having an anterior keel on the horn cores, rather divergent horn cores in anterior view, the braincase still more strongly angled on the face axis, and wide orbital rims. He also (1904 : 87) established a subfamily Pseudotraginae to include *Protoryx*, *Pseudotragus* and *Pachytragus* along with *Eotragus* (=*Eocerus*), *Protragocerus*, *Miotragocerus*[1] and *Neotragocerus*. His definition of the new subfamily (1904 : 85) included the characters of strongly compressed goat-like horns and a long narrow face, and *Palaeoryx* remained a hippotragine.

Andree (1926) referred new material to *Protoryx carolinae*, founded a new species *P. crassicornis*, a new variety *laticeps* of *P. carolinae*, and a new variety *tenuicornis* of *P. hentscheli* Schlosser. He founded a new species of *Pachytragus*—*P. schlosseri*, referred a skull to *Pseudotragus capricornis* Schlosser, and founded a new species *longicornis* of *Pseudotragus*. Finally he referred one fossil skull to *Hippotragus* as the new species *H. kopassi*. He followed Schlosser's consignment of the genera into Pseudotraginae and Hippotraginae.

Pilgrim & Hopwood (1928 : 27, 30) selected *P. carolinae* as the type species of *Protoryx* with Gaudry's skull in Paris as holotype. They added to *P. carolinae* two Pikermi skulls, BM(NH) M.10839 and M.11415, and one from Samos, M.4198, as well as two Lausanne skulls, 298 and 362, which Major (1894 : 28, 30) had labelled '*P. gaudryi*'. They reduced *P. crassicornis* Andree to a variety of *P. carolinae*, but raised his variety *laticeps* of *P. carolinae* to species level, assigning to it Lausanne skulls 28 and 201 and the maxilla 580 and Schlosser's (1904 : 48) frontlet of *P.* cf. *carolinae*. They considered that Schlosser's and Andree's records of *P. carolinae* were not conspecific with Gaudry's type skull or the other material they had just assigned themselves to this species, and used for it Major's name *P. longiceps* with the Lausanne skull 22 as holotype and the Maragha skull BM(NH) M.3841 as paratype. Finally they took a skull in Lausanne, 30, labelled *P. hippolyte* as the type of a new variety of Schlosser's *Pseudotragus capricornis*.

Bohlin (1936 : 17, 18) transferred the two London skulls M.10839 and M.11415 from *Protoryx carolinae* to the related genus *Palaeoryx*, suggested confining the specific name *carolinae* to the actual Paris specimen and using *P. gaudryi* as the name for

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[1] I thank Q. B. Hendey for telling me of a paper by Kretzoi (1968) in which it is pointed out that the familiar generic names *Tragocerus* Gaudry 1861 and *Microtragus* Andree 1926 for fossil antelopes are definitely preoccupied by beetles. Kretzoi proposed the new name *Sporadotragus* in place of *Microtragus*. For *Tragocerus* the next available name seems to be *Miotragocerus* Stromer. This name was published in 1928; *Graecoryx*, which I believe could have been applied to the same genus, was published by Pilgrim and Hopwood at some date close to 28th June 1928. This was the date at which the copy of their book in the Palaeontology Library of the British Museum (Natural History) was accessioned. In this paper I shall use *Miotragocerus* in place of the junior homonym *Tragocerus*.

Samos '*P. carolinae*', i.e. the Lausanne skulls 298 and 362. He thought the London Samos skull M.4198 was not a *Protoryx*, but he assigned to *Protoryx* many specimens previously put elsewhere: Andree's specimens of Schlosser's *Pseudotragus capricornis*, of *Pseudotragus longicornis*, *Pachytragus schlosseri* and *Hippotragus kopassi*, and Pilgrim and Hopwood's *Pseudotragus capricornis* var. *hippolyte*. There was no skull from Pikermi which agreed with any of the Samos *Protoryx*, and this threatened a nomenclatorial revision since the type cranium of *Protoryx carolinae* was a Pikermi fossil. None the less he continued to use the genus *Protoryx* for Samos specimens, although he considered that they represented a group which, like *Chilotherium* Ringström and *Samotherium* Major, never spread as far as Pikermi. He attempted no revision at the species level, but did propose that *Palaeoryx* could not be in a separate family (=tribe of Simpson's 1945 classification) from *Protoryx*. From this it seemed to follow that they would all pass into the Hippotragini, and that the group 'Pseudotraginae' in which they were wrongly linked with *Eotragus*, *Protragocerus*, *Miotragocerus* and *Neotragocerus* would be abolished. Already in his work on Chinese lower Pliocene Bovidae Bohlin (1935c : 119) had doubtfully referred the two genera, with some related Chinese forms, to Hippotragini. Neither Pilgrim (1939 : 26–27) nor Gentry (1967 : 266) challenged this view, but Sokolov (*in* Orlov 1968 : 537) had doubts. It is now the purpose of this paper to interpret *Pachytragus* and possibly *Protoryx* as members of the tribe Caprini, and *Palaeoryx* as an ovibovine. Although I do not place all three genera in one tribe, there is no doubt that in the lower Pliocene time level they were closely related.

Palaeoryx, *Protoryx* and *Pachytragus* differ from the contemporaneous and commonly fossilized boselaphine *Miotragocerus* by not having a stepped anterior keel, by having horn cores less strongly compressed medio-laterally, a braincase more strongly angled on the face axis and without temporal ridges on its dorsal surface, a higher infraorbital foramen, a wider mastoid exposure of the periotic, and smaller foramina ovalia.

Skull characters shared by *Palaeoryx*, *Protoryx* and *Pachytragus* are horn cores without transverse ridges or torsion; the postcornual fossa, lying postero-laterally to the horn core base, is shallow or altogether absent; the braincase top is at an angle to the line of the face axis; the parieto-frontals suture has only a slight anteriorly directed indentation centrally or none at all; temporal lines are not developed as strong ridges and do not approach one another very closely; the supraorbital pits are small; the preorbital fossa is large and shallow and sometimes has an upper rim; the back edge of the infraorbital foramen is fairly high over P^{2-3} or P^3; the median indentation at the back of the palate is level with the lateral ones or passes slightly anterior to them; the mastoid exposure of the periotic has a moderate or large area; posteriorly the ventral edge of the auditory bulla may pass downwards where it meets the front of the paraoccipital process; there are no goat folds (anterior transverse flanges) on the lower molars; the lateral lobes of the lower molars are not drawn out transversely. These characters could be considered for inclusion in the definition of any tribe or subfamily to which the three genera belong.

Genus ***PALAEORYX*** Gaudry

1861a *Palaeoryx* Gaudry : 241.
1861b *Palaeoryx* Gaudry : 393.

Type species. *Antilope pallasi* Wagner, 1857 : 149, pl. 9, fig. 21.

Generic diagnosis. As for the species.

Palaeoryx pallasi (Wagner)

1857 *Antilope pallasi* Wagner : 149, pl. 9 fig. 21.
1861a *Palaeoryx pallasi* Gaudry : 241.
1861b *Palaeoryx speciosus* Gaudry : 393, pl. 9 figs 1–3.
1865 *Palaeoryx pallasi* Gaudry : 271, pl. 47 figs 1–5.
1894 *Palaeoryx rotundicornis* [nom. nud.] Major : 24.
1904 *Palaeoryx majori* Schlosser : 38, pl. 7 figs 1–5.
1926 *Palaeoryx laticeps* Andree : 161, pl. 13 figs 4, 4a, 6.
1928 *Palaeoryx woodwardi* Pilgrim & Hopwood : 77, pl. 6 fig. 1.
1928 *Palaeoryx woodwardi* var. *columnatus* Pilgrim & Hopwood : 78.

Lectotype. The cranium at Munich figured by Wagner, and designated by Pilgrim & Hopwood (1928 : 75). It has survived the Second World War.

Localities. Pikermi, Samos.

Age. Lower Pliocene.

Diagnosis. Moderate to large sized antelopes with a low and wide skull; horn cores are of short to moderate length, little compressed medio-laterally, without keels, set fairly obliquely in side view and widely apart, moderately divergent in anterior view, tips reapproaching slightly; braincase is short and wide; orbital rims are moderately projecting; frontals between the horn bases are a little higher than the orbital rims; mid-frontals suture is not raised; mid-frontals and parieto-frontals sutures are not usually complicated; sides of braincase are generally parallel, but sometimes widening anteriorly or posteriorly; supraorbital pits are set widely apart; ethmoidal fissure is present; zygomatic arch is deep at its anterior end where it passes beneath the orbit; back edge of tooth row is slightly anterior to the level of the front of the orbit.

Occipital surface faces almost uniformly backwards; the median vertical occipital ridge is well marked and the hollows on either side of it moderately so; the anterior tuberosities of the basioccipital are set rather widely apart; basioccipital usually has some indication of a central longitudinal groove; foramina ovalia are moderately sized; auditory bulla is small to moderate sized and moderately inflated.

Brachyodont cheek teeth; enamel may be somewhat rugose; basal (or accessory) pillars are moderate-sized to small on lower molars and small to absent on uppers; there are indentations into the back edge of the rear central cavities of the upper molars; the rear of the front medial lobe and the front of the rear medial lobe on the upper molars fuse only relatively late in wear; styles are not very prominent on upper molars or premolars; ribs between parastyle and mesostyle of upper molars are sometimes strong; premolar row is long with scarcely reduced front premolars.

REMARKS. *Previously named specimens.* The horn cores of the lectotype diverge rather less than is normal in the species, and this was partly the reason for founding some of the synonymous species names. However some other fossils have previously been referred to *Palaeoryx pallasi.* These are a skull from Pikermi now in Paris which was figured by Gaudry (1865 : 271, pl. 47 fig. 1); a Lausanne specimen, 198, from Samos with part of its left horn core and most of the braincase; a Münster skull referred to by Andree (1926 : 160, pl. 15 fig. 7) with rather a narrow cranium and small horn cores, probably a female; a cranium from Pikermi in the Vienna museum labelled *P. pallasi*; and a Pikermi skull and cranium, BM(NH) M. 10831 and M.11426, referred to *P. pallasi* by Pilgrim & Hopwood (1928 : 76). M.11426 has its horn core perhaps badly stuck on but certainly curving strongly backwards, and it is M.10831 which indicates the presence of an ethmoidal fissure in this species. The skull of *P. pallasi* from Maragha (Mecquenem 1924 : 31, pl. 4 fig. 1) is really a *Miotragocerus* as noticed by Bohlin (1936 : 14), and there is no other convincing evidence of *Palaeoryx pallasi* from Maragha. I have not seen the two Stuttgart skulls mentioned by Andree (1926 : 160, pl. 12 fig. 8) as possibly females of *P. pallasi.*

The Lausanne skull, 200, of *Palaeoryx rotundicornis* Major has already been referred by Pilgrim & Hopwood (1928 : 75) to *P. pallasi.* A Lausanne cranium with horn core bases, 29, was also taken as *P. rotundicornis* by Major (1894 : 18), but is also *P. pallasi.* The anterior tuberosities of the basioccipital of 29 are rather wider apart than in 200.

The cranium of *P. majori* Schlosser (1904, pl. 7 figs 5, 5a, 5b) in Munich has fairly straight, very divergent horn cores which show considerable inward curvature at the tips. According to the diagnosis the orbits are situated entirely beneath the horn cores, but this character is difficult to use in bovids with such obliquely inserted horns, and I could not see that any difference existed between this species and the lectotype of *P. pallasi.* The horn core characters, larger braincase, rounded orbits, and supposedly smaller primitive teeth do not justify a separate specific name. Andree (1926 : 161) placed a Samos cranium in Vienna, 1911.v.9, in *P. majori*, and this too can be taken as *P. pallasi.* Schlosser (1904 : 43, pl. 8 figs 3–5) also founded a species *Palaeoryx ingens* on teeth, but I would not be certain that they even belong to *Palaeoryx* (see also p. 239). The holotype of Andree's *P. laticeps* is a cranium with a low wide braincase, horn cores rather strongly curved backwards, thick and robust. These, and other linked characters given in his diagnosis essentially amount to a wide skull and backward horn core curvature, and are insufficient to carry the specimen beyond a likely range of variation for *P. pallasi.*

P. woodwardi, BM(NH) M.10832, was alleged by Pilgrim & Hopwood to differ from *P. pallasi* in its more divergent and narrower horn cores, which with the frontals are smaller relative to the rest of the skull. The horn cores certainly are small but all that this and other invoked characters demonstrate is a less robust skull which is possibly of a female. It is true that there are no basal pillars on the upper molars, but teeth assigned by Schlosser (1904, pl. 7 fig. 1) to *P. majori* have a small basal pillar only on M^2. The greater divergence of the horn cores in this species agrees with those called *laticeps* and *majori*, but there is not the inward curvature of the tips. The variety *columnatus* of *P. woodwardi* was based on a Lausanne skull 199 and a London palate M.11416. The palate was noted to be too wide for *Protoryx carolinae* [but was mistakenly assigned to that species on another page (Pilgrim & Hopwood 1928 : 30)]. Basal pillars are present on all molars, as in most upper molars of *Palaeoryx pallasi*, and the supposed hypsodonty and weak development of mesostyles are insufficient to separate it from *P. pallasi*. The preserved right horn core of 199 is very narrow, widely divergent with little inward curving at the tip, and set obliquely.

Palaeoryx pallasi is not represented by skulls, crania or frontlets in the Samos collection of the American Museum of Natural History.

Infraspecific variation

I have not found differences between the Samos and Pikermi representatives of this species, but there is a fair amount of individual variation. Thus the Vienna specimen from Samos shows a flattening of the lateral surface of the horn cores. The mid-frontals sutures are complicated in the London and Vienna skulls from Pikermi but less so in Lausanne skulls 29 and 200 from Samos; the frontals-parietal suture has almost no central indentation in the Lausanne skulls but more in others. The braincase widens anteriorly in the Munich skull from Samos and in BM(NH) M.10831 from Pikermi, but in Lausanne 200 and the Münster specimen figured by Andree (1926, pl. 13 figs 4, 6) it widens slightly posteriorly, and in BM(NH) M.10832 and both Vienna skulls its sides are nearly parallel. The back edge of the infraorbital foramen is high over the middle or back of P^3 in M.10831 and Lausanne skulls 199 and 200, but over the P^{2-3} junction in the Paris example. The Münster specimen shown in Andree (1926, pl. 15 fig. 7) has the median indentation at the back of the palate behind the level of the lateral ones. The occipital median ridge and flanking hollows are quite strongly developed in Lausanne skull 198. In 29 the strong median ridge gives the appearance of the occipital surface facing two ways. The basioccipital has a central longitudinal groove in most pieces but not in Lausanne 29 (Pl. 1 fig. 2) and 200. Moderately sized foramina ovalia may be seen in Lausanne 198 and BM(NH) M.10831, and larger ones in the Münster skull figured by Andree (1926, pl. 13 figs 4, 6). The downturning of the lower edge of the auditory bulla into the paraoccipital process is seen in Lausanne 29 (Pl. 1 fig. 1) and in the Münster skull figured by Andree (1926, pl. 13 figs 4, 6). Both specimens have quite small auditory bullae, that of 29 perhaps more inflated than in the Münster specimen. The bulla of the other Münster skull (Andree 1926, pl. 15 fig. 7) is slightly larger and the back does not pass down into the paraoccipital process.

Some mean skull measurements of *Palaeoryx pallasi*, together with ranges, standard deviations and coefficients of variation are shown on Table 2 p. 258. With individuals coming from both Pikermi and Samos and with the possibility of female animals having been included, there are high coefficients of variation.

Tooth characters

The upper teeth of *Palaeoryx pallasi* are known from the London skulls M.10831 and M.10832, the Paris skull illustrated by Gaudry (1865, pl. 47 fig. 1), the Lausanne skulls 199 and 200, and from the skull in Münster illustrated by Andree (1926, pl. 15 fig. 7). They are distinguished from teeth of the similarly sized Samos ovibovine *Criotherium argalioides* Major by the latter's rounded medial lobes of the upper molars and premolars, massive P^2, relatively long and narrow upper molars, lower premolars with transversely-running rather than diagonal front and back edges, the somewhat rounded outline of worn lateral lobes of the lower molars, not very outbowed medial walls of the lower molars, their straighter central cavities, and the small basal pillars set away from the main body of the tooth.

They are more difficult to distinguish from *Miotragocerus*. Even their great size is not decisive, since a larger species of *Miotragocerus* than *M. amalthea* is known from Samos and Maragha (p. 243 below). This animal, which is quite definitely not a *Palaeoryx* by the lack of bending of its braincase, its temporal ridges, its horn cores being medio-laterally compressed at least in their higher parts, fails to show even the distinctive large P^2 of the smaller *Miotragocerus* species.

Individual dentitions

Even complete upper or lower dentitions are very difficult to identify unless they are attached to complete skulls or associated with horn cores. The palate which Roth & Wagner (1855 : 452, pl. 14 fig. 1) described as *Antilope speciosa* may belong to *P. pallasi* or to some other species. It is not identifiable from the illustration, although Gaudry (1861a : 240; 1861b : 393) took it as the same species as *P. pallasi*.

In the Munich collection the upper dentition figured by Schlosser (1904, pl. 7 fig. 1) as *Palaeoryx majori* can perhaps be assigned to *P. pallasi*. The late joining up of the back of the front lobe of M^2 can be seen, and the incipient bilobing of P^3 is slightly less than it appears on the drawing. By the relative sizes of individual premolars this is slightly more likely to be *Palaeoryx* than a large *Miotragocerus*. The deciduous premolars and lower molar shown in pl. 7 figs 2 and 3 could be *P. pallasi*, but I would not identify them thus with certainty. The lower dentition of pl. 7 figs 4, 4a is more likely to belong to a *Miotragocerus* by the large size of its P_2 and the shallowness of the ramus. The Munich teeth assigned by Schlosser (1904, pl. 8 figs 3, 4, 5) to *Palaeoryx ingens*, supposedly differed from *P. pallasi* by their large size and molars with more angular crescents. The generic attribution is doubtful, but if it were correct there would be no reason to separate the teeth from *P. pallasi*. The basal pillars on the lower molars stand clear of the body of the tooth.

A large palate from Pikermi in London, BM(NH) M.11416, was figured by Pilgrim & Hopwood (1928, pl. 5 fig. 1, 1a) as *Palaeoryx woodwardi* var. *columnatus*, and is very large, as much so as AMNH 20587. As with the above specimens there is the difficulty of deciding whether it might be referable to a large *Miotragocerus* species.

A possible specimen of *Palaeoryx pallasi* teeth in New York is AMNH 20587 from quarry 5. It is a large palate in which the permanent premolars are just coming into wear. The molars have strong ribs between their parastyles and mesostyles such as exist in the *Palaeoryx pallasi* skull BM(NH) M.10831 and tapered and pointed medial lobes, the premolars are narrower than in *Criotherium*, there are no basal pillars, there are indentations into the rear central cavities of the M^2s; in no molars are the medial lobes joined to one another or to the lateral side of the tooth in its centre, and the infraorbital foramen is above the back of P^3. The P^4s are somewhat twisted in their sockets, a distortion also seen in the next palate below. The brachyodonty can be assessed from the measurements: height of mesostyle on little worn M^3 from the base of the enamel = 20·3 and length = 26·4 at the occlusal surface and 29·7 as the maximum at a lower level.

AMNH 20751 is another palate from quarry 4, with rather more worn teeth than the above. The left P^2 is absent (present in life), the left P^4 is twisted in its socket, and some molars are damaged. It is a smaller palate than 20587, P^2 may be relatively smaller and P^3 is certainly smaller than in 20587. Other characters are narrow and pointed medial lobes, no basal pillars, strong ribs between parastyle and mesostyle, no spurs into central cavities (at this stage of wear), mesostyles less marked (again at this state of wear), infraorbital foramen above back of P^3.

AMNH 20643 from quarry 1 is a very damaged palate; all teeth except the right P^2 have survived but only the left P^2 and right M^3 are undamaged. The teeth are well worn although the molars still have their central cavities. The basal pillars are small, and the left M^2 shows what was probably a strong rib between parastyle and mesostyle.

AMNH 86627 from quarry 1 is a palate in middle wear with all its teeth except the left P^2, but slight damage to some teeth. It is a little smaller than the previously mentioned fossils, and does not have strong ribs between parastyle and mesostyle. There are very small basal pillars on M^2 and M^3.

AMNH 86465 a left P^3–M^3 and 86570 a left upper molar from quarry 1 could also belong to *Palaeoryx pallasi*.

A number of fossils in Lausanne may belong to *P. pallasi*: a right rather worn maxilla, 519, a worn left mandible 411 with P_2–P_4 and the anterior part of the medial wall of P_4 closed, a left mandible 888 with P_3–M_1, a left mandible fragment 1095 with a broken M_1 and $M_2 + M_3$, and a right mandible fragment 1264 with M_2 and M_3. However the identity of the mandibles is not certain, and lower tooth characters were not included in the diagnosis of *Palaeoryx pallasi*.

There are also dentitions in the Münster collection which could belong to *P. pallasi*.

COMPARISONS. Bohlin (1935c : 138, text-figs 119–126) refers to *Palaeoryx sinensis* and *Palaeoryx* sp. from the Chinese lower Pliocene. He wrote that *P. sinensis* was so close to *P. majori* (here included in *P. pallasi*) that it could be the same species. The same would probably apply to *Palaeoryx longicephalus* Sokolov (1955 : 219, fig. 2) from the upper Miocene or lower Pliocene of Novocherkassk. We may conclude that the single species *P. pallasi* or a superspecies of which it was part was widespread in the lower Pliocene. *Sinoryx bombifrons* Teilhard de Chardin & Trassaert (1938, pl. 1 fig. 5, text-figs 37, 38) could also belong here; the pictures of it much resemble a crushed cranium of *Palaeoryx pallasi*, 1122, in Lausanne, except that its tooth row may be placed too posteriorly. *Palaeoryx athanasiui* Simionescu (1922 : 452; 1930 : 121, 145, text-figs 60–66, pl. 4 figs 2, 3, pl. 5 fig. 1) from the Romanian site of Măluşteni of Plaisancian age is later than other *Palaeoryx*. Its tooth row is also rather too posterior for it to be satisfactory as *Palaeoryx*, although its small central incisors support the idea of it as some kind of caprine.

Genus ***PROTORYX*** Major

1891a *Protoryx* Major : 609.
1892 *Protoryx* Major *in* Stefani, Major & Barbey : 94.

TYPE SPECIES. *Protoryx carolinae* Major, 1891a : 608.

GENERIC DIAGNOSIS. The type species is the only one here included in the genus. It is known only from Pikermi.

Protoryx carolinae Major

1865 Antilope d'espèce indéterminée. Gaudry : 289, pl. 52 fig. 1.
1891a *Protoryx carolinae* Major : 608.
1928 *Protoryx carolinae* Major. Pilgrim & Hopwood : 30, pl. 3 figs 1, 3.

HOLOTYPE. The cranium from Pikermi in Paris figured by Gaudry.

LOCALITY. Pikermi.

AGE. Lower Pliocene.

DIAGNOSIS. Differs from *Palaeoryx pallasi* in its slightly smaller size. The skull is high and narrow rather than low and wide; horn cores are long, somewhat compressed in the medio-lateral plane, with a tendency to a flattened lateral surface, widest posteriorly, without keels, more uprightly inserted in side view than in *Palaeoryx pallasi* and appearing to insert less posteriorly, set closer together at their bases, not very divergent in anterior view, strongly curving backwards, horn core tips scarcely reapproach; sides of the braincase are more or less parallel; the braincase is narrow in dorsal view; orbital rims project moderately; the frontals are a little higher between the horn bases than are the orbital rims; the mid-frontals suture is not very raised; the mid-frontals and parieto-frontals sutures are not very complicated; supraorbital pits are set widely apart; the large ethmoidal fissure is not narrow (BM(NH) M.11415); zygomatic arch is deep anteriorly (BM(NH) M.11415); tooth row may be less anteriorly placed than in *Palaeoryx pallasi*; each half of the occipital surface tends to face partly laterally as well as backwards; basioccipital is narrow perhaps with a less clear central longitudinal groove than in *Palaeoryx pallasi*; moderately large auditory bulla. Tooth characters as in *Palaeoryx pallasi*.

Remarks. The differences of *Protoryx carolinae* from *Palaeoryx pallasi* very largely amount to a narrower skull (Text-fig. 1) and associated features such as narrower, more uprightly inserted and backwardly curved horn cores. Otherwise, and particularly in its tooth characters, there is very little difference. The holotype cranium and left horn core in Paris and two skulls in London are all from Pikermi. The Paris specimen shows clearly that the frontals, including the horn pedicel, are hollowed, and is not preserved sufficiently far anteriorly to show the supraorbital pits.

Pilgrim & Hopwood (1928 : 32) provisionally assigned to *P. carolinae* a Samos skull with mandibles, atlas and axis vertebrae, BM(NH) M.4198. Bohlin (1936 : 3) rejected this identification, and I follow him. The braincase of this skull is hardly

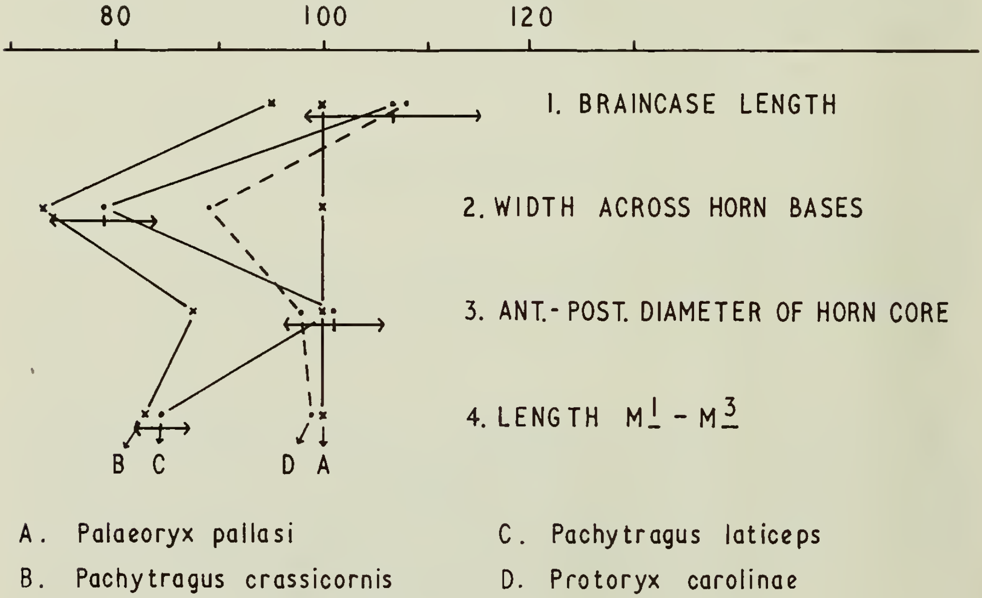

Fig. 1. Percentage diagram of the means of four measurements on skulls belonging to the *Palaeoryx-Pachytragus* group of antelopes. *Palaeoryx pallasi* has been used for the standard line at 100%; the mean readings for other species are expressed as percentages of the mean reading in *P. pallasi*. Both Pikermi and Samos specimens contribute to the readings for *P. pallasi*, and tooth measurements were taken only from identified skulls. The maximum numbers of readings for each species were: *P. pallasi* 11, *Protoryx carolinae* 3, *Pachytragus laticeps* 25, *P. crassicornis* 13, but the full number of readings was not available for every measurement. Horizontal lines show the extent of the standard deviations for *P. laticeps*. Note the slightly smaller size and narrow skull of *Protoryx carolinae* compared with *Palaeoryx pallasi*, the rather large horns in *Pachytragus laticeps* compared with *Protoryx carolinae*, and that the teeth of *Pachytragus crassicornis* are only a little smaller than in *P. laticeps*.

at all angled on the face axis, and I believe that it belongs to the Boselaphini. Along with a number of other skulls in various collections from Samos and Maragha, it is likely to be a species related to *Miotragocerus amalthea* but somewhat larger. *Prodamaliscus gracilidens* Schlosser (1904 : 29, pl. 4 fig. 6, pl. 6 fig. 4) may also have been this species, but the specimen was probably destroyed during the Second World War. Pilgrim & Hopwood (1928 : 30) had *P. carolinae* at Samos on the basis of Lausanne skulls 298 and 362, but Bohlin (1936 : 4) has already pointed out that 362 is a *Miotragocerus*, and I accept neither skull as *P. carolinae* (see p. 250 below). The Pikermi mandibles in London referred by Pilgrim & Hopwood (1928 : 32) to *P. carolinae* could well be of that species, but I would not be certain of the identification.

COMPARISONS. It is interesting that *Protoryx carolinae* shows some similarities to ?*Protoryx planifrons* from the Chinese lower Pliocene of Kansu described by Bohlin (1935c : 119, text-figs 88–91, pl. 15 fig. 5). It is not likely, so far as I can see, that ?*P. shansiensis* Bohlin (1935c : 123, text-figs 92–94) or ?*Protoryx* sp. (Bohlin 1935c : 125, text-figs 95, 96) are distinct species from ?*P. planifrons*. This Chinese species agrees with *Palaeoryx pallasi* and with *Protoryx carolinae* in being a large antelope, its supraorbital pits set widely apart, the parieto-frontals and mid-frontals sutures not very complicated, possibly a deep zygomatic arch anteriorly, the molar teeth not very hypsodont, with basal pillars and long premolar rows. In addition it resembles *P. carolinae* in the fairly upright horn core insertions, the relative height of the skull, and in the greatest width of the horn core section lying posteriorly, but a central longitudinal groove on the basioccipital and perhaps the divergence of the horn cores take it closer to *Palaeoryx*. With its especially massive horn cores and notably small supraorbital pits it must represent an East Asian development of the *Protoryx* stock unparalleled at more western sites. The skull M.1295 in Uppsala of ?*Protoryx shansiensis* has a thick parietal bone and an extremely small and narrow ethmoidal fissure.

There is no reason to suppose that the antelopes referred in the same paper to *Prosinotragus* and *Sinotragus* (Bohlin 1935c : 130, 133) are other than a more extreme development from the same ancestry as *Protoryx planifrons*. Their horn cores have become very short and thick, compressed with an anterior keel above, with a clockwise torsion in the right horn core, a short braincase much angled on the face, wide nasals, a quadrangular basioccipital, small foramina ovalia, and small to moderately inflated auditory bullae, but still a large preorbital fossa and rather unadvanced teeth. It is interesting that clockwise torsion in the right horn core has developed in this stock as well as in the smaller *Oioceros*. *Protoryx carolinae* could be an ancestor or a western ancestral-like member of this group. In this case the ultimate nomenclatorial procedure would be to extend the name *Protoryx* to the whole Chinese group, and not to sink a monospecific *Protoryx carolinae* in *Palaeoryx*.

Paraprotoryx founded by Bohlin (1935c : 126, figs 97–104) for other Chinese specimens with a fairly well rounded horn core section, is probably related to *Protoryx*.

Genus ***PACHYTRAGUS*** Schlosser

1904 *Pachytragus* Schlosser : 56.

Type species. *Pachytragus crassicornis* Schlosser, 1904 : 56.

Generic Diagnosis. Smaller than *Palaeoryx* or *Protoryx*; skulls are fairly narrow; horn cores are moderately long to long, medio-laterally compressed, more uprightly inserted even than in *Protoryx* and appearing to rise more directly above the orbits than in *Palaeoryx*, set closer together, little divergent, the widest part of their transverse section lying mid-way along their antero-posterior diameter, hollowed close to their bases; frontals are higher between the horn bases than in *Palaeoryx* or *Protoryx*; mid-frontals suture is rather raised; mid-frontals and parieto-frontals sutures are quite complicated; braincase has parallel sides or widens anteriorly; supraorbital pits are less small and less widely spaced than in *Protoryx carolinae*; nasals are long, domed and have a narrowly drawn out back suture; ethmoidal fissure is long and narrow; zygomatic arch has not deepened anteriorly; occipital surface is in two planes with each half facing partly laterally as well as backwards; basioccipital is narrow; foramina ovalia are small to moderate; auditory bullae are moderate to large; the ventral edge of the bulla may pass downwards posteriorly on to the front edge of the paraoccipital process, instead of rising to make the join.

The teeth are more hypsodont than in *Palaeoryx pallasi* or *Protoryx carolinae*; their enamel is only slightly rugose; basal pillars are very small or absent on upper molars and small on lower molars; there is no late joining of the medial lobes of the upper molars; the upper molars have a strong mesostyle with a tendency for the lateral wall behind to acquire a concave section; the rib between parastyle and mesostyle is not strong; medial walls of lower molars are little outbowed between the stylids; premolar row is short; styles are fairly strong on upper premolars; hypoconid of P_4 is quite pointed so that the lateral wall in front of it appears indented; metaconid of P_4 is rather bulbous in middle wear; paraconid of P_4 is not joined with the metaconid to close the anterior part of the medial wall; P^2 smaller than in *Palaeoryx pallasi* and *Protoryx carolinae.*

Contained species: *Pachytragus crassicornis* Schlosser, the type species.
Pachytragus laticeps (Andree).

Remarks. The most important difference of *Pachytragus* from the antelopes previously considered, and the one which principally justifies its generic rank and indicates the origin of a new adaptive zone (definition of Simpson 1953 : 201) is its advanced teeth. The diagnostic features of these teeth are illustrated in Text-fig. 5. A more stable support for the horn cores of *Pachytragus* is perhaps indicated by the decline of the anteriorly deepened zygomatic arch. *Pachytragus* as conceived here contains many specimens formerly placed in *Protoryx*.

Pachytragus laticeps (Andree)

1891a *Protoryx carolinae* (in part) Major : 608.
1891a *Protoryx longiceps* [nom, nud.] Major : 608.

1891a *Protoryx gaudryi* [nom. nud.] Major : 608.
1891a *Protoryx hippolyte* [nom. nud.] Major : 608.
1904 *Protoryx carolinae* Major. Schlosser : 45, pl. 9 fig. 8.
1904 *Protoryx* cf. *carolinae* Schlosser : 48.
1924 *Protoryx carolinae* Mecquenem : 33, pl. 5 figs 3, 4.
1926 *Protoryx carolinae* Andree : 151, pl. 12 figs 3, 3a, 4.
1926 *Protoryx carolinae* var. *laticeps* Andree : 153, pl. 12 figs 5, 9.
1926 *Protoryx hentscheli* Schlosser. Andree : 154, pl. 12 fig. 2, pl. 13 fig. 9.
1926 *Protoryx hentscheli* var. *tenuicornis* Andree : 155, pl. 12 fig. 6, pl. 13 fig. 2.
1926 *Protoryx crassicornis* Andree : 156, pl. 12 fig. 1, pl. 13 fig. 8.
1926 *Hippotragus kopassi* Andree : 158, pl. 15 figs 8, 10.
1928 *Protoryx longiceps* Pilgrim & Hopwood : 34, pl. 3 figs 2, 2a, pl. 5 figs 2, 2a.
1928 *Protoryx carolinae* var. *crassicornis* Andree. Pilgrim & Hopwood : 33.
1928 *Pseudotragus capricornis* var. *hippolyte* Pilgrim & Hopwood : 40.
1928 *Protoryx laticeps* Andree. Pilgrim & Hopwood : 36, pl. 4 figs 1–3.

HOLOTYPE. The skull in Münster figured by Andree (1926, pl. 12 figs 5, 9).

LOCALITIES. Samos, Maragha.

AGE. Lower Pliocene.

DIAGNOSIS. Horn cores are relatively larger than in *Protoryx carolinae*, moderately long, compressed medio-laterally, without keels, strongly curved backwards, sometimes more strongly bent back at the tips than lower down; orbital rims are narrow to moderately wide; braincase is sometimes long; median occipital ridge and its flanking hollows are frequently only poorly marked; the basioccipital has a central longitudinal groove.

REMARKS. The smaller size and relatively larger horn cores of *Pachytragus laticeps* than *Protoryx carolinae* can be seen in Text-fig. 1. The increased horn size must be linked with other differences from *Palaeoryx* and *Protoryx*, for instance that the horn cores have acquired more upright insertions and a more curved course in profile, thereby distributing their increased weight equally over each side of the occipital condyle-atlas pivot.

The illustrated paratype of this species is the Maragha skull BM(NH) M.3841. The Paris skull of *Pachytragus* from Maragha (Mecquenem 1924 : 33, pl. 5 figs 3, 4) also belongs here; its horn cores diverge about as much as in the holotype but are shorter. The back of the nasals is narrow, there is a long and narrow ethmoidal fissure, and the preorbital fossa lacks an upper rim.

Long-brained and short-brained varieties

In some examples, for which Pilgrim & Hopwood (1928 : 34) used Major's name *Protoryx longiceps*, the horn cores are larger, more medio-laterally compressed, less divergent and with tips which do not reapproach, the width across the top of the skull in the region of the horn bases is smaller, the braincase longer, the occipital surface higher and the median occipital ridge and its flanking hollows less marked. This is a more extreme change from the putative *Palaeoryx* or *Protoryx*-like ancestors. In the graphs of Text-figs 2–4 I have indicated by a separate symbol the specimens assigned by Pilgrim & Hopwood to the name *longiceps* as well as others which seemed to fit the criteria just mentioned. It can be seen that there is only imperfect separation from other *Pachytragus laticeps* in horn core compression, braincase length and relative narrowness across supraorbital pits and horn bases. It is probable that temporally or geographically separate natural populations have contributed to the *P. laticeps* material as it exists in museum collections today.

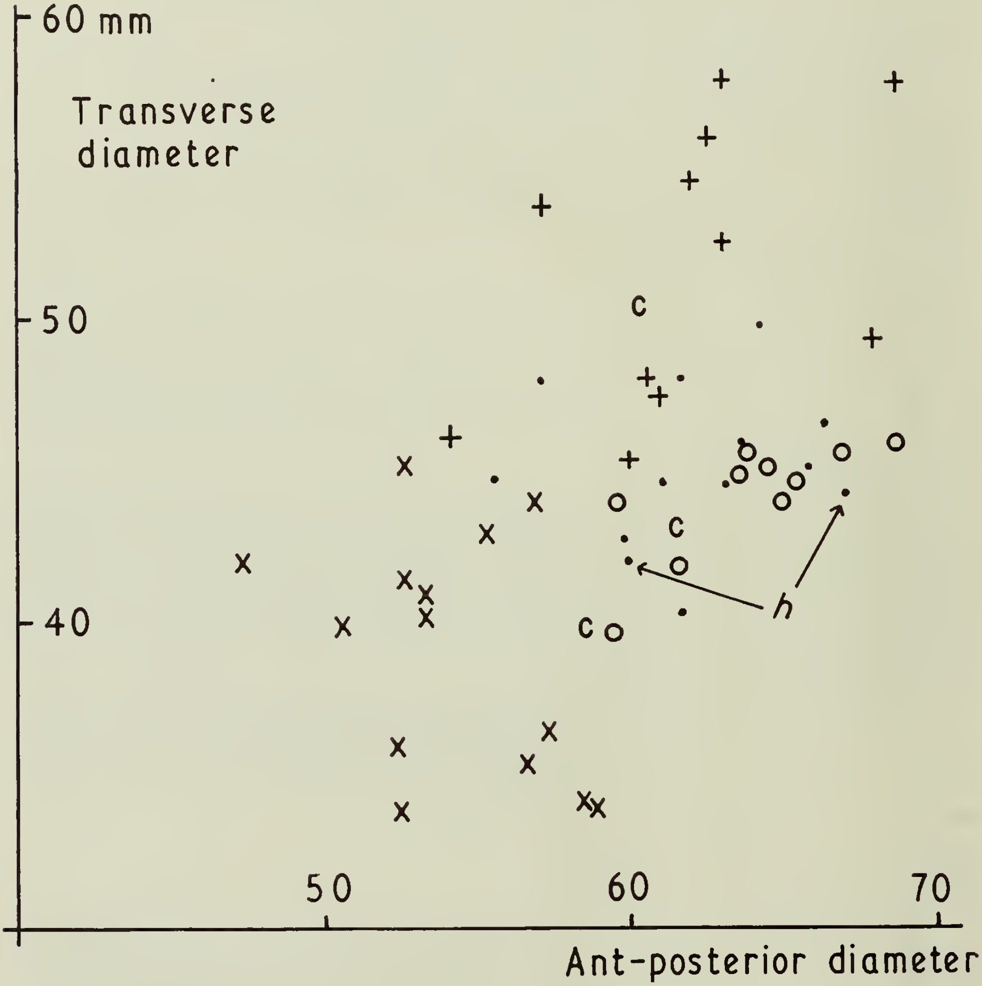

FIG. 2. Graph of horn core compression. The readings were taken at the base of the horn cores immediately above the pedicel. *Palaeoryx pallasi* has large and little compressed horn cores, those of other species are more medio-laterally compressed, and in *Pachytragus crassicornis* they are also smaller. + = *Palaeoryx pallasi*, c = *Protoryx carolinae*, · = *Pachytragus laticeps*, o = longer crania of *P. laticeps*, x = *P. crassicornis*, *h* = two Lausanne specimens of '*Protoryx* '*hippolyte*.

It is impossible to sort out the members of these original populations, and it would be unwise to assume that only two such populations have been sampled, one for each extreme of the range of variation. For this reason I shall not use the trivial name *longiceps* as a trinomial.

The means of some skull measurements, and their ranges, standard deviations and coefficients of variation for *Pachytragus laticeps* are shown in Table 2 on p. 258. Despite the inclusion of the long-brained individuals of this species, the coefficients of variation are generally less high than in the smaller sample of *Pachytragus crassicornis*.

The cranium with horn cores at Lausanne, 22, was that which Pilgrim & Hopwood (1928 : 28) believed Major had intended to be the holotype of *Protoryx longiceps*. The tips of its horn cores are not sharply bent backwards, the frontals above the left orbit are hollowed, the mid-frontals suture is not raised, the sides of the braincase are parallel or even widening anteriorly, the large mastoids are visible, the anterior tuberosities of the basioccipital are not large and flank a central longitudinal groove

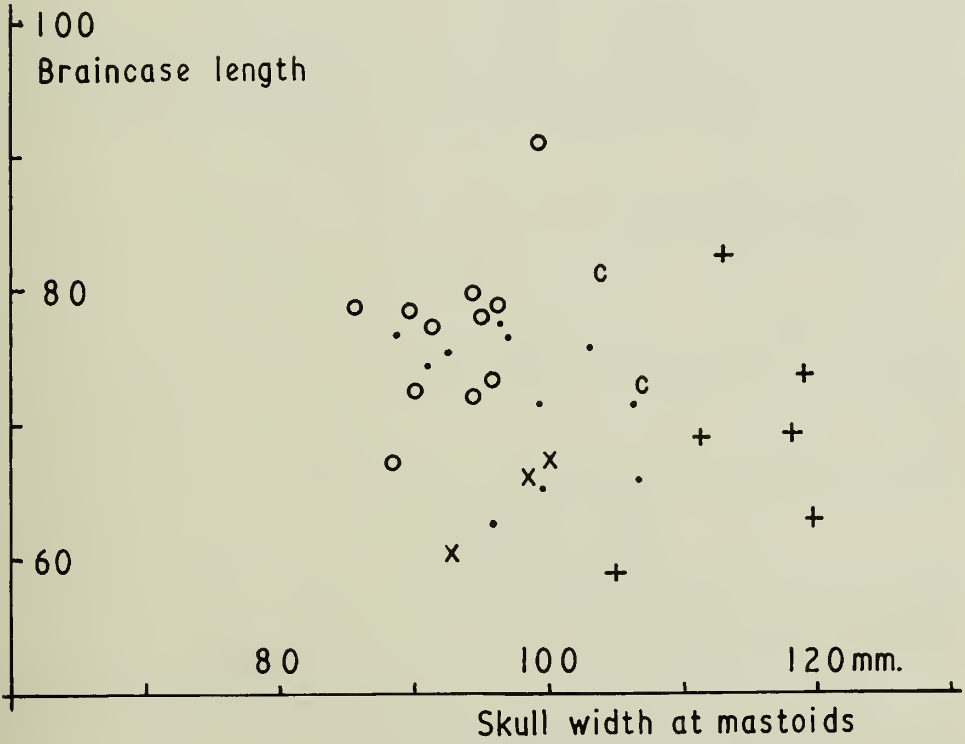

Fig. 3. Graph of braincase length against skull width across the mastoids. This graph indicates the size and relative narrowness of the cranium. Braincase length is measured from the mid-dorsal point of the parieto-frontals suture to the top of the occipital surface. Symbols as in Text-fig. 2.

(Pl. 2 figs 1, 2). The median vertical ridge on the occipital is not marked, but the left and right sides of the bone face partly laterally. The Lausanne cranium 26 is very similar except for the more localized raising of its frontals between the horn bases.

Protoryx carolinae of Schlosser (1904 : 45) is a long-brained *Pachytragus laticeps*. The braincase is parallel sided and there is a large mastoid. The face fragment used in his pl. 9 fig. 8 cannot be fitted to the cranium; in fact a part of the posterior end of the face is not shown in the illustration.

Examples of long-brained *P. laticeps* in the American Museum of Natural History are as follows. 20612 from quarry 1 is a cranium with lower parts of the horn cores in which the apparent length of the braincase may have been increased by the use of plaster. 20621 also from quarry 1 is a cranium with lower part of the right and almost complete left horn core; it is the only New York specimen with an auditory bulla and the bulla shows the downward connection to the front of the para-occipital process. It also has small to moderate-sized foramina ovalia. 20645 from quarry 1 is a cranium with horn cores. 20649 from quarry 1 is a frontlet with lower parts of horn cores. 20690 from quarry 1 is a cranium with well preserved horn cores showing abrupt bending back of the tips. 22783 from block H in quarry 1 is a cranium with the right horn core and part of the left; the left one was sectioned approximately 20 mm above the pedicel top and showed spongy central parts (Pl. 2 fig. 4). 23037 from quarry 4 is a cranium with complete horn cores, bent

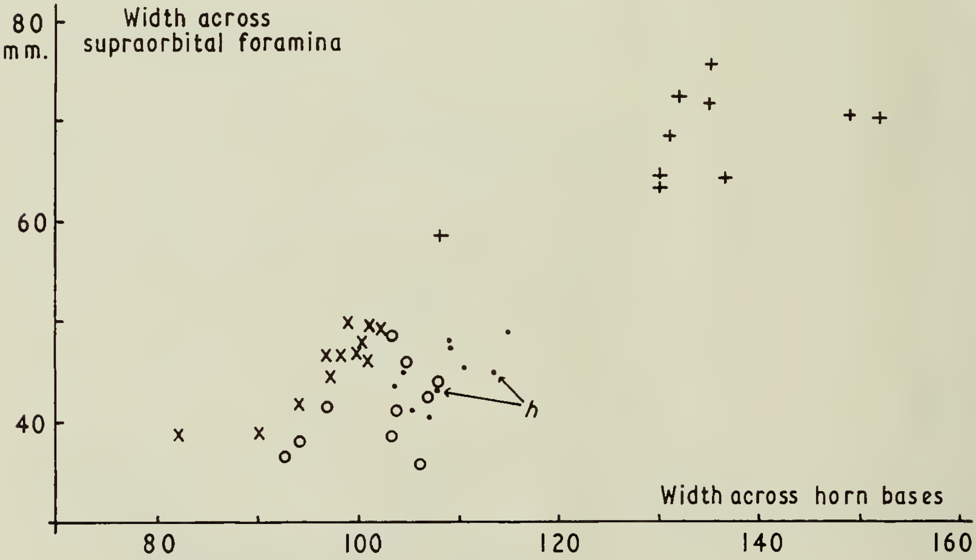

Fig. 4. Width across supraorbital foramina compared with width across narrowest part of lateral walls of horn pedicels. Symbols as in Text-fig. 2. Among *Pachytragus* it is *P. crassicornis* which has the widest separation of supraorbital foramina, and is closest to later goats.

back at their tips. 23038 from quarry 1 is a cranium with the lower parts of its horn cores. The right one was sectioned at about 10 mm above the pedicel top and showed a clear central hollowing (Pl. 2 fig. 3).

The Lausanne cranium 20453 has rather a long braincase, and also has a hollowing at the base of its left horn core.

Andree's *Hippotragus kopassi* in Münster is also rather long-brained. It has a narrow ethmoidal fissure, parallel sides of its braincase, small foramina ovalia, the ventral edge of its auditory bulla rises posteriorly where it meets the paraoccipital process, and it has preserved its dentition and rather high face. Andree (1926 : 158, 159) used this skull to show the closeness of *Hippotragus* to his *Protoryx* group of the Pseudotraginae (=*Pachytragus* as used in this paper). The narrow and high face, strong bending of the braincase on the face, and the high insertions of the large transversely compressed horn cores impressed him as distinctive characters, but it did not appear to me that any substantial difference existed between this skull and other *Pachytragus laticeps*.

The holotype cranium of *Pachytragus laticeps* does not have a particularly long braincase. It has parallel sides of its braincase, and the ventral edge of the left auditory bulla descends to meet the front edge of the paraoccipital process.

A well preserved *P. laticeps* skull on public exhibition in the Natural History Museum in Basle is an excellent example of the shorter-brained form of this species. Its horn cores approach having an anterior keel in the middle of their course. Although the M^1s have already lost their central cavities, there are indications of transverse ridges across the dentine of the molars' occlusal surfaces, which suggests use of the cheek teeth in a way similar to goats and sheep.

The shorter-brained Lausanne cranium 201 (Pilgrim & Hopwood 1928, pl. 4 figs 1, 1a) is a *P. laticeps*, but the lack of a central longitudinal groove on its basioccipital makes it more like the species to be described next. Its occipital surface is lower and wider than in the long-brained Lausanne cranium 22, and the sides of its braincase are parallel. A Lausanne frontlet 28 (Pilgrim & Hopwood 1928, pl. 4 fig. 2) has no anterior keels and rather diverging horn cores, and is probably from a shorter-brained *P. laticeps*.

I have not seen the material of *Protoryx* cf. *carolinae* of Schlosser (1904 : 48), but I include it with the shorter-brained *Pachytragus laticeps*, following his description and Pilgrim & Hopwood's (1928 : 36) placing.

The shorter-brained Münster skull which Andree (1926 : 156, pl. 12 fig. 1, pl. 13 fig. 8) called *Protoryx crassicornis* shows quite compressed horn cores with large bases, a high face, a braincase widening slightly anteriorly, moderate-sized foramina ovalia, and a moderately-developed median occipital ridge and flanking hollows. The illustration in front view shows reapproaching horn core tips, now lost. The differences which Andree noted from other skulls here included in *Pachytragus laticeps*, valid as they may be between individuals, do not carry the skull beyond the morphological range within which it could be considered conspecific. There was certainly no reason for Pilgrim & Hopwood (1928 : 33) to link this skull with *Protoryx carolinae* which they had principally built around Pikermi specimens, for this skull is smaller, its horn cores insert more uprightly, and the teeth are like those of other Samos skulls. Andree's own text (1926 : 156) emphasizes this point about the teeth.

Shorter-brained *Pachytragus laticeps* in the American Museum of Natural History are the following. As with the long-brained variety, none come from quarry 5. 20674 from quarry 1 is a cranium with left horn core strongly bent back at its tip and with the lower part of the right horn core. 20691 from quarry 1 is a cranium with the lower parts of both horn cores. 20707 from block E in quarry 1 is a partly cleaned skull without the front of its face. Both its horn cores are broken at the level of the top of the pedicel and hollowed internally. The long narrow ethmoidal fissures and back part of the nasals are visible. 20770 from 100 yards west of Mytilini village is a cranium with horn core bases. 20777 from 100 yards west of the same village is a rather small left horn core with an inwardly deflected tip. 22857 from quarry 4 is a cranium with horn cores. 86580 is a frontlet with horn cores, and it is labelled 'block Y' but without a quarry number. 86583 of unknown quarry is a damaged cranium with horn cores broken at their bases and clearly hollowed.

I have not been able to assign all *P. laticeps* to the shorter or longer brained varieties. Doubtful specimens in New York are 20609 from quarry 1 which is a face without premaxillae or the right nasal but showing the lachrymal and jugal sutures, 20598 from quarry 1 a cranium with horn core bases, 20673 from quarry 1 the base of a right horn core and a left horn core with skull fragments, 20778 and 20779 two frontlets with horn core bases from 100 yards west of Mytilini, and 86450 a frontlet with horn cores. The Lausanne frontlet 27 is another doubtful specimen.

Other skulls and crania

The Lausanne cranium 298 is interesting; it was labelled as *Protoryx gaudryi* by Major and referred to *P. carolinae* by Pilgrim & Hopwood (1928 : 30). It is considerably damaged and has been repaired with glue and plaster; it agrees with the species to be described next in its keels and diverging horn cores, but is rather large and has a wide shallow longitudinal groove on its basioccipital. No measurements could be taken because of the damage.

The other Lausanne cranium, 362, which they also referred to *P. carolinae* belongs to *Miotragocerus* as shown by its temporal ridges with rugose surface in between, the occipital surface in one plane only, the horizontal top edge of the occipital in rear view, rather narrow mastoids, and large foramina ovalia.

The most difficult specimen to assess at Lausanne is the cranium, 30, of '*Protoryx hippolyte*' (Pl. 3 figs 1, 2), referred to as a variety of Schlosser's *Pseudotragus capricornis* by Pilgrim & Hopwood (1928 : 40). However it is too large to belong to that species, does not show the relatively very large horn cores of the presumed male skull, and the supraorbital pits are set closer together. At first sight it appears that the braincase is little bent on the face axis but this is probably due to distortion, the back of the braincase having been pushed forwards against the horn bases. There is strong medio-lateral compression of the horn cores, their divergence increases evenly towards the tips, and they appear rather uprightly inserted in side view. Their appearance of having been short and having had an anterior keel may result from damage caused by weathering. The *Pachytragus* skull in Basle shows that the angle of the parietal to the occipital surface here is not too small for *P. laticeps*. The occipital surface is low and wide as in most *P. laticeps*, and it has a weak median ridge without hollows on either side. The front of the basioccipital is missing but there was a well marked central longitudinal groove. From these characters and its size this specimen can be provisionally included in *P. laticeps*.

Another Lausanne specimen, the frontlet 31, much resembles the cranium just discussed.

Protoryx hentscheli was founded by Schlosser (1904 : 49) on teeth of *Pachytragus*. The syntypes in Munich were supposed to differ from teeth of '*Protoryx carolinae*' (=*Pachytragus laticeps* as used here) by weaker styles and ribs on the molars, smaller premolars, the anterior position of the vertical indentation on the lateral side of P_3 and P_4, the weaker indentation on the medial lobes of P^2 and P^3, and the weaker development of medial cusps on P_3 and P_4. These, and other differences mentioned by Pilgrim & Hopwood (1928 : 38) seem valid only between individuals. It is impossible to assign the teeth specifically; that they belong to *Pachytragus* is all I would be prepared to say. The name *Protoryx hentscheli* was subsequently extended by Andree to a nearly complete skull, and the name *P. hentscheli* var. *tenuicornis* to a cranium, both in Münster. The nearly complete skull is very interesting in that it shows some characters divergent from other *Pachytragus*: frontals only a little raised between horn bases, rather a low face, the tooth row set rather anteriorly; all this recalls *Palaeoryx pallasi*. Otherwise it appears to be an example of the normal fairly short brained *P. laticeps* with horn cores diverging in the middle of their course and reapproaching towards the tips. The cranium of var. *tenuicornis* agrees with the above skull in what characters are available, and its broken left horn core shows a hollowed pedicel. Although these skulls are an apparently primitive variation of *Pachytragus laticeps*, I do not consider them worth naming, and certainly there is no case for applying to them Schlosser's specific name *hentscheli*, based on indeterminate teeth. They illustrate what an early form of *Pachytragus* could have been like. I have retained these two pieces within *P. laticeps*, and have not supposed that they belong to an actual ancestral species. They suggest that *Pachytragus* could derive from *Palaeoryx* or a *Palaeoryx*-like ancestor, perhaps some antelope not dissimilar to *Protoryx carolinae*.

A skull from Salonica assigned to *Protoryx carolinae* by Arambourg & Piveteau (1929b : 105, pl. 7 fig. 6, 6a) probably belongs to this species. Its closely inserted horn cores are without keels, the brain widens anteriorly in dorsal view, temporal lines are wide posteriorly, the nasals are narrowly drawn out posteriorly and have no lateral flanges anteriorly, and large premaxillae rise with even width to a definite contact with the nasals. These characters at the front of the face are probably common to the whole genus *Pachytragus*, if not to *Palaeoryx* and *Protoryx* as well.

A female skull

In the New York collection is a *Pachytragus* skull with small horn cores, 20687 from quarry 1 (Pl. 3, fig. 3). It is presumably a female. It is complete except for premaxillae, most of the nasals, a part of the left postorbital bar, and the right postorbital bar and zygomatic arch. The horn cores are of very small basal diameter (30·2 × 22·0, right), somewhat medio-laterally compressed, set rather obliquely and with a concave front edge in profile, inserted close together and diverging little in anterior view. Connected with the smallness of the horn cores is the strong slope of the orbital rims. The preorbital fossa is only shallow (they are normally smaller in females), neither supraorbital pits nor infraorbital foramina are visible, the frontals between the horn bases are hardly higher than the orbital rims, the maxilla is deep above the tooth row, and the occipital surface is clearly in two planes. The skull's provenance in quarry 1 would seem to rule out its assignation to *P. crassicornis*. An awkward question is why there are no other female skulls in any Samos collections. A left horn core AMNH 20777 is very like a horn core of *P. laticeps* and is an alternative candidate for representing females among the fossils. Its basal diameters are about 49 × 38 mm.

Tooth characters and individual dentitions

The teeth of *Pachytragus laticeps* may easily be told from those of *Palaeoryx pallasi* and *Protoryx carolinae* by their smaller size and advanced morphology. Smaller size distinguishes them from the unnamed large *Miotragocerus* represented by AMNH 23036, BM(NH) M.4198 and other specimens, and their advanced characters from all *Miotragocerus*. Teeth of *Miotragocerus* are less hypsodont, they retain larger basal pillars (*a*) and a later joining together of the medial lobes of the upper molars (*b*), the mesostyle on the upper molars is less marked (*c*), the medial walls of the lower molars are more outbowed between the stylids (*d*), the premolar row is longer and anterior premolars larger, hypoconid of P_4 is not pointed (*e*), metaconid of P_4 is less bulbous but has a large backwardly turned medial flange (*f*), and the paraconid of P_4 is larger relative to the parastylid (*g*). The characters indicated by letters (*a*) to (*g*) are illustrated in Text-fig. 5, and a *Pachytragus* palate is photographed in Pl. 4 fig. 2.

Very many upper and lower dentitions of *Pachytragus* are known, and I will comment only on previously misidentified specimens. The teeth shown by Schlosser (1904, pl. 9) may all be taken as belonging to either this species or the next. The teeth of pl. 9 figs 2, 3, 5, 6 and 7 had been used to establish the species *Protoryx hentscheli*, supposedly having weaker ribs and styles, rounded inner lobes, a large metastyle on M^3, a triangular rear lobe of M_3, and rugose enamel. These characters, in so far as they are detectable at all, are inadequate to remove the teeth from assignation to *Pachytragus laticeps* or to the next species. Since it is doubtful which of the two they belong to, I have not listed *P. hentscheli* as of Schlosser (1904) among the synonyms of *P. laticeps*. Skulls which Andree later assigned to *P. hentscheli* have been included in *P. laticeps*.

The right upper dentition 578 in Lausanne, listed by Major (1894 : 35) as '*Protoryx* sp.' is really a *Miotragocerus*.

Pachytragus crassicornis Schlosser

1904 *Pachytragus crassicornis* Schlosser : 56, pl. 11 fig. 11.
1926 *Palaeoryx* cf. *stützeli* Andree : 162, pl. 14 figs 1–3.
1926 *Pseudotragus longicornis* Andree : 147, pl. 10 figs 2, 3.
1926 *Pseudotragus capricornis* Schlosser. Andree : pl. 13 fig. 7.
1926 *Pachytragus schlosseri* Andree : 148, pl. 12 fig. 7, pl. 13 fig. 3.

Lectotype. The frontlet described and figured by Schlosser (1904 : 56, pl. 11 fig. 11) was designated by Pilgrim & Hopwood (1928 : 43). *Pachytragus crassicornis* is the type species of its genus.

Locality. Samos.

Age. Lower Pliocene.

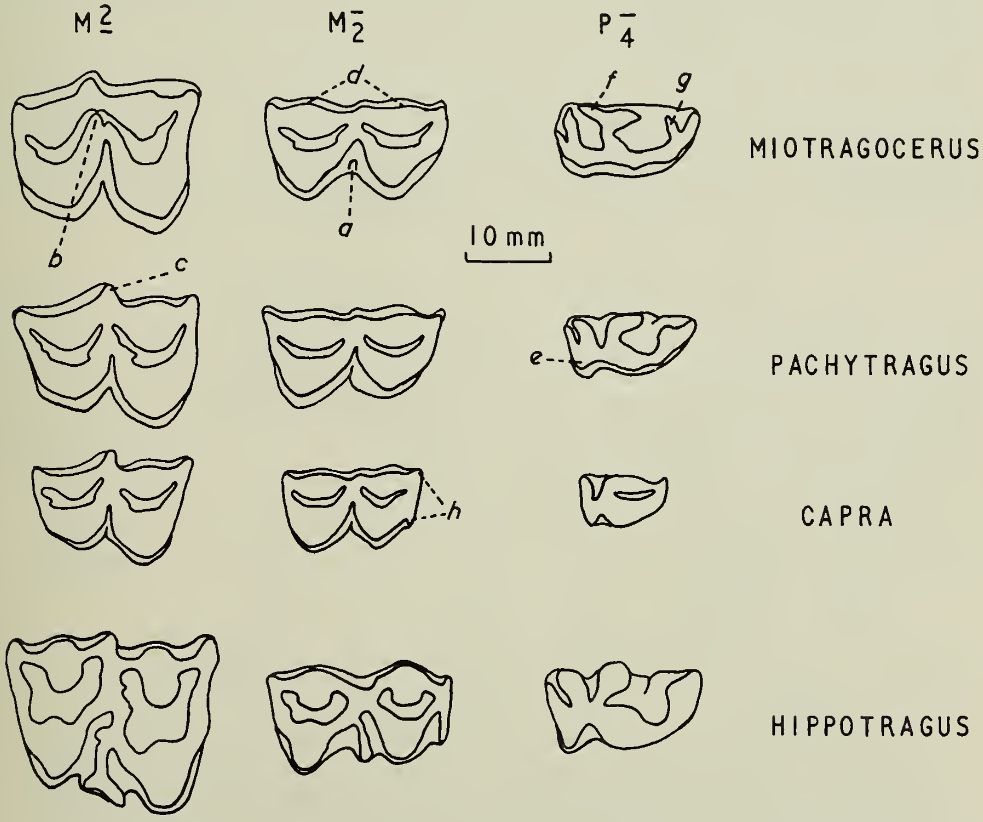

Fig. 5. Occlusal views of cheek teeth of the right side, their anterior edges being towards the right. Explanation in text, p. 252, and *h* = goat fold.

DIAGNOSIS. Smaller than *Pachytragus laticeps*; horn cores are slightly smaller and shorter, often more medio-laterally compressed, with an anterior keel, insertions less upright than in *P. laticeps* but more than in *Protoryx carolinae*, divergence greater and increasing toward the tips instead of tending to reapproach at the tips, less curved backwards in side view; orbital rims are rather wide; braincase top is fairly long and set at a steeper angle to the occipital surface; tooth row set more posteriorly than in *Palaeoryx pallasi*; median occipital ridge is often prominent and with deeper flanking hollows; basioccipital has fairly localized anterior tuberosities and thus little development of a central longitudinal groove; teeth are no smaller than in *P. laticeps* despite the overall size reduction.

REMARKS. By its smaller overall skull size unaccompanied by any substantial diminution of tooth size *P. crassicornis* is evidently adapted to a harsher environment than *P. laticeps*. It differs additionally from that species by its shorter less backwardly curved horn cores with anterior keels, and the tooth row is now definitely placed rather posteriorly. Profile views of this species in comparison with others are shown in Text-fig. 6, anterior views of horn cores in Text-fig. 7, and sections across horn cores in Text-fig. 8.

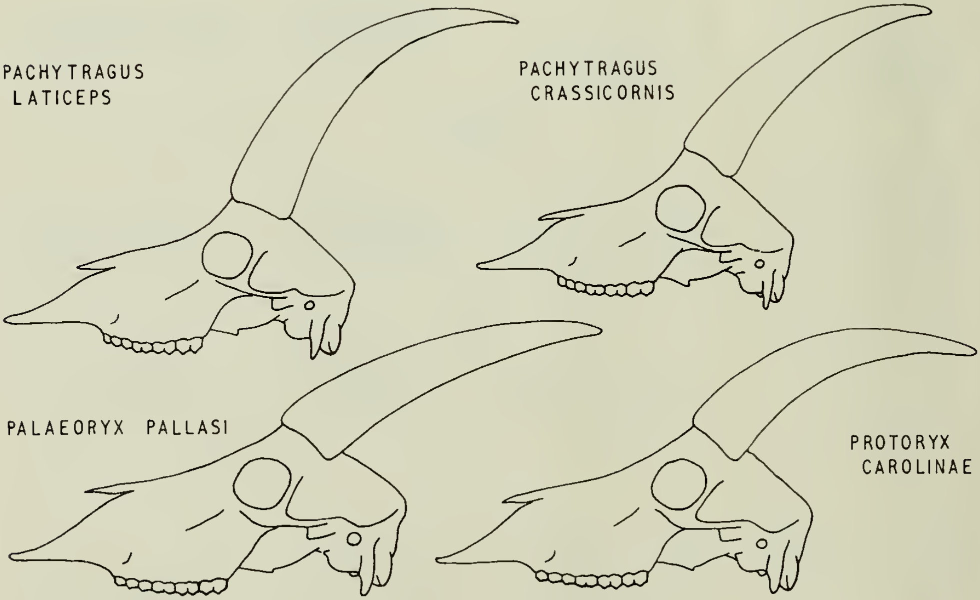

FIG. 6. Reconstructions of side views of skulls of *Palaeoryx*, *Protoryx* and *Pachytragus*. The figures are in scale with one another. Notice the inclination and curvature of the horn cores and deep anterior part of the zygomatic bars in *Palaeoryx pallasi* and *Protoryx carolinae*; the anterior positioning of the tooth row in *Palaeoryx pallasi*; that the teeth of *Pachytragus crassicornis* have not diminished below the size of those of *P. laticeps*; and the differing inclinations and curvatures of their horn cores.

The lectotype of *Pachytragus crassicornis* Schlosser (1904 : 56, pl. 11 fig. 11) shows strong bending of the braincase on the face axis (the appearance of this being exaggerated by distortion), the orbital rims would have been wide when complete, and the upper parts of the right horn core are sufficiently preserved to show the anterior keel.

Individual skulls and crania

The following specimens in the American Museum of Natural History are all from Brown's quarry 5 with one exception. 20567 is part of a skull with braincase, right horn core, part of the right side of the face, the right P^3 to M^3 and the left P^4 to M^3. 20568 is a more or less complete skull lacking only the front of its face; it has the left P^2 to M^3 and the right P^3 to M^3, and a long and thin ethmoidal fissure. 20569 (Pl. 4 fig. 1) is most of a skull lacking parts of the right orbit, nasals, premaxillae and parts of the basioccipital; it has the right P^3 to M^3 and left P^2 to M^3. 20579 is another more or less complete skull, lacking only nasals and premaxillae; it is probably the best preserved skull of the species in existence. The ethmoidal fissures are long and thin, and the teeth present are the right P^2 to M^3 and the left M^1 to M^3. 20708 is from quarry 1 but agrees better with *P. crassicornis* than with *P. laticeps*; it is a cranium without the right horn core or parts of the lower occipital surface. 22938 is a cranium with both horn cores intact. 22939 is a cranium with both horn cores. 22940 and 22943 are frontlets with most of the right horn core and part of the left. 22948 is a damaged cranium with a somewhat distorted right

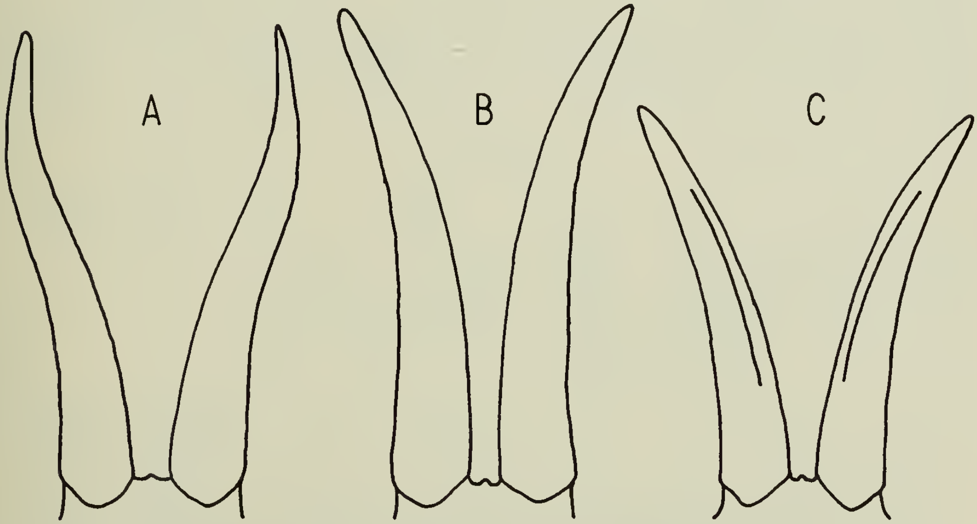

FIG. 7. Anterior view of the horn cores of (*A*) *Pachytragus laticeps*, (*B*) long-brained variety of *P. laticeps*, (*C*) *P. crassicornis*. The figures are in scale with one another. Notice in (*B*) compared with (*A*) that the horn cores are larger, less divergent, and with tips which do not reapproach. *P. crassicornis* has anterior keels.

horn core and part of the left one. 22949 is a cranium with horn cores on which part of the left preorbital fossa is visible.

A number of other named specimens in European museums can best be placed in this species, although their inclusion widens the range of variation within the species. As with the long-brained examples of *P. laticeps*, no conception of what was happening to the species in time can be hoped for without more geological knowledge of the Samos deposits. The first of these specimens is the skull of *Pseudotragus capricornis* in Münster described by Andree (1926 : 146, pl. 13 fig. 7) but not conspecific with the skull for which Schlosser (1904 : 51, pl. 10 figs 7, 8) had first used the name. Andree's specimen shows short medio-laterally compressed horn cores diverging from one another and with anterior keels, the braincase probably widening anteriorly, but the basioccipital not clearly with less developed longitudinal ridges behind the anterior tuberosities than in *Pachytragus laticeps*. There is a slight tendency towards transverse wear ridges across the dentine of the upper molars as in goats and sheep. I have not seen the Stuttgart skull fragment which Andree refers to (1926 : 146) under this name, but the Münster one differs from *Pseudotragus capricornis* by its greater size, anterior keel, and relatively larger teeth and face.

The almost complete skull of *Pachytragus schlosseri* Andree (1926 : 148, pl. 13 fig. 3) is in Vienna and is certainly rather small. It has been much restored with

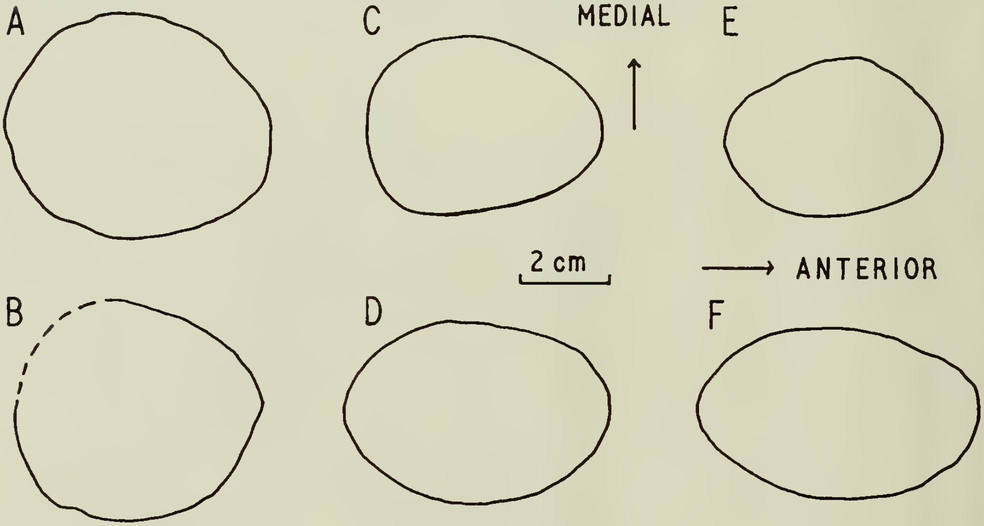

Fig. 8. Sections of right horn cores taken at a distance above the pedicel top equal to half the antero-posterior diameter at the base of the horn core. A = *Palaeoryx pallasi* from Samos figured by Schlosser (1904, pl. 7 fig. 5); B = *Megalovis latifrons*, a left horn core (Se 1483) in Basle reversed for this drawing; C = *Protoryx carolinae* BM(NH) M.11415; D = *Pachytragus laticeps*, a skull in Basle; E = *P. crassicornis* AMNH 22938 reversed for this drawing; F = the long brained variety of *P. laticeps* AMNH 23037.

plaster on the alisphenoid flanges, the right zygomatic bar, the top of the postorbital bars, and the top of the occipital surface. It is the restoration of the top of the postorbital bars which has given a wrong impression of narrow orbital rims. Also in the dentition picture (Andree 1926, pl. 14 fig. 4) the large metastyle of M^2 should have been shown as the parastyle of M^3. The horn cores are somewhat compressed, their triangular cross section as shown by Andree does not extend much above their base, they are quite strongly divergent in anterior view, there is a small ethmoidal fissure, the small and shallow preorbital fossa has a trace of an upper rim, the infraorbital foramen is high above the front of P^3 on the left and the back of P^3 on the right, and the median indentation at the back of the palate is behind the level of the lateral ones. The skull is probably closer to this species than to *P. laticeps* by its rather small size, latero-medial compression of horn cores without reapproach of the tips, and the quite strong divergence of the horn cores. But the horn cores lack keels, and the condition of the occipital surface cannot be clearly seen.

The cranium in Münster assigned to *P. schlosseri* by Andree (1926, pl. 12 fig. 7) is similarly difficult to assign. It has no anterior keel on the horn cores, but it does have divergent short horn cores, and the frontals between the horn cores are well raised. The braincase probably widened anteriorly.

Pseudotragus longicornis of Andree (1926, pl. 10 figs 2, 3) is in Vienna. The lateral surface of its horn cores is somewhat flattened, the back of the nasals is just a little in front of the level of the front of the orbits, the moderate sized preorbital fossa has a slight upper rim, the infraorbital foramen is above the front of P^3. It is like *Pachytragus crassicornis* in its small size, strong medio-lateral compression higher up its horn cores with which is linked the tendency to an anterior keel, and the shape of the anterior tuberosities of the basioccipital with barely any central longitudinal groove. The lesser divergence of the horn cores, and their backward

TABLE I

	Antero-posterior diameter of horn core	Latero-medial diameter of horn core	Minimum width across lateral sides of horn pedicels	Width across lateral edges of supraorbital foramina	Length M^1–M^3	Length P^2–P^4
Pseudotragus capricornis (Andree pl. 13 fig. 7)	52·6	33·7	—	39·8	55·1	—
Pachytragus schlosseri (Andree pl. 13 fig. 3)	47·3	42·0	101·4	49·7	56·6	39·3
Pachytragus schlosseri (Andree pl. 12 fig. 7)	56·8	43·9	98·3	46·4	—	—
Pseudotragus longicornis (Andree pl. 10 figs 2, 3)	52·7	45·2	97·0	c.46·5	53·5	38·1
Palaeoryx cf. *stützeli* (Andree pl. 14 figs 1, 3)	55·3	43·0	97·3	c.44·3	—	—

curvature are more like *P. laticeps*, but in the width of its orbital rims and the hollowings of the occipital surface the Vienna animal is intermediate.

The frontlet in Vienna which Andree assigned to *Palaeoryx* cf. *stützeli* agrees well with his specimens of '*Pseudotragus longicornis*' and '*Pachytragus schlosseri*'. It is not conspecific with the example of *Palaeoryx stützeli* Schlosser (1904, pl. 8 fig. 6) in Munich which is a *Sporadotragus*; this specimen is of a larger animal, it lacks the anterior surface on its horn cores and has less extreme bending down of the face on the braincase. The orbital rims are moderately to strongly projecting, the lateral surface of the horn cores is a little flattened, and there is possibly an approach to having a keel higher up on the right, but it is too damaged to be certain.

Those skulls described by Andree which I believe to be *Pachytragus crassicornis* have the following measurements shown in Table 1 on p. 257, which I made myself and used in the Text-figures.

Some skull measurements for *Pachytragus crassicornis* are shown in Table 2 below. Coefficients of variation are rather high in comparison with the low numbers of measured individuals; this is because of the difficult skulls just discussed.

TABLE 2

	Number measured	Mean	Range	Standard deviation	Coefficient of variation
Antero-posterior diameter of horn core at base	10	62·3	54·2–68·7	4·08	6·55
	23	62·9	57·0–68·9	2·99	4·75
	13	54·1	47·3–58·7	3·34	6·17
Latero-medial diameter of horn core at base	10	51·6	45·3–57·9	4·90	7·55
	24	44·5	35·4–49·8	3·34	7·52
	13	38·7	33·5–45·2	4·02	10·40
Minimum width across lateral surfaces of horn pedicels	11	133·5	108·2–152·0	11·33	8·49
	21	105·6	94·4–123·6	6·71	6·36
	10	97·7	82·2–102·5	5·95	6·09
Width across lateral edges of supraorbital pits	10	68·1	58·6–75·9	5·23	7·68
	21	43·0	36·5–49·0	3·73	8·77
	13	45·6	38·6–49·8	3·56	7·80
Braincase length from back of frontals to top of occipital	10	69·5	59·2–82·8	7·13	10·26
	17	75·5	65·3–91·2	5·89	7·81
	6	66·8	60·1–75·3	5·13	7·69
Skull width across mastoids behind auditory meatus	6	114·3	105·0–119·8	5·72	5·01
	22	95·4	85·8–106·8	5·60	5·87
	5	93·5	85·7–100·3	6·10	6·52
Length M^1–M^3	6	67·6	61·9–69·9	3·00	4·44
	18	57·6	54·4–61·0	1·84	3·19
	15	56·8	53·5–60·6	2·12	3·74
Length P^2–P^4	4	50·1	46·2–52·6	—	5·62
	9	38·0	35·1–41·9	2·13	5·60
	9	37·2	34·0–39·3	1·60	4·29

For each measurement the top line shows the readings for *Palaeoryx pallasi*, the middle line for *Pachytragus laticeps*, and the last line for *P. crassicornis*.

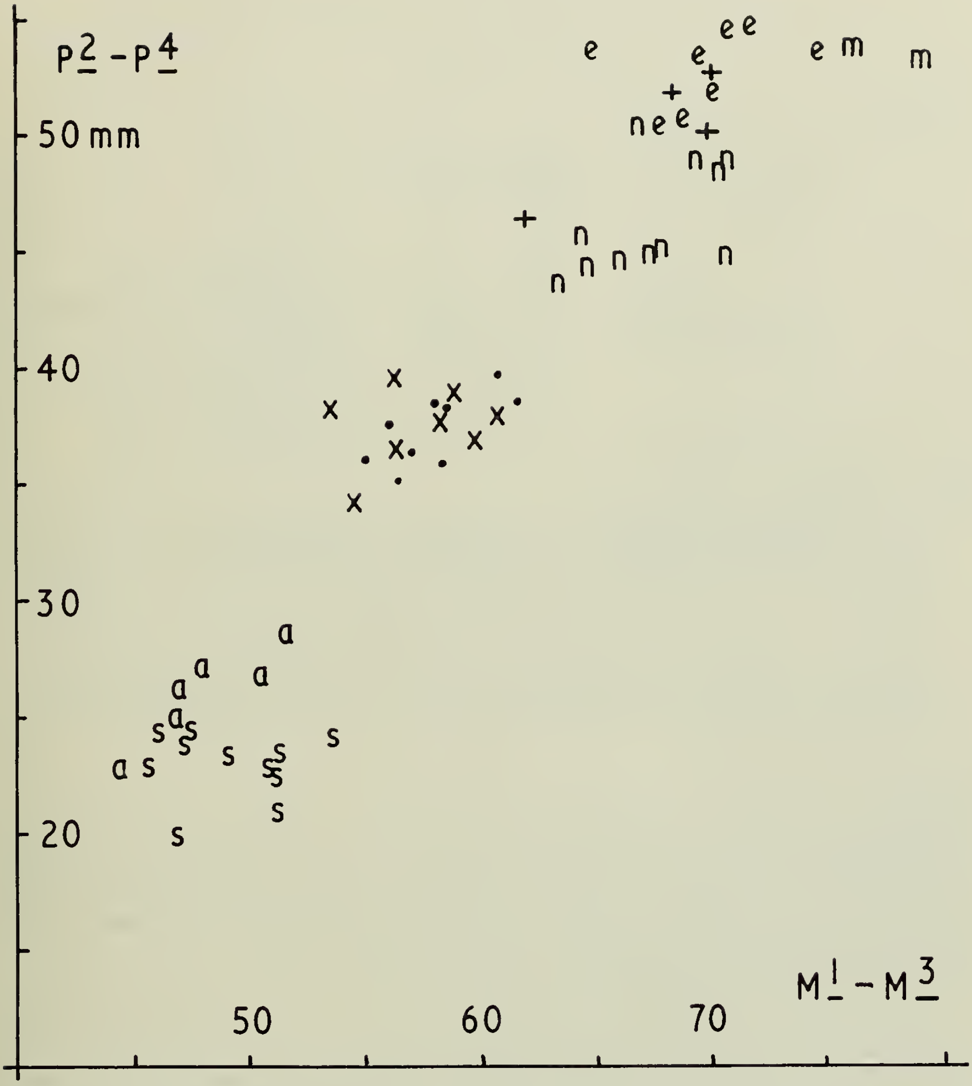

FIG. 9. Graph of the length of the upper premolar row plotted against length of upper molar row. Symbols as in Text-fig. 2 except that no separate symbol is used for the long brained *Pachytragus laticeps*, e = *Hippotragus equinus*, n = *H. niger*, s = *Capra sibirica*, a = *C. aegagrus*, and m = *Megalovis latifrons*. Tooth measurements were taken on identified skulls, and in addition one *Pachytragus* dentition from Brown's quarry 5 in New York was taken as *P. crassicornis* and four from quarries 1 and 4 as *P. laticeps*. Notice that the two *Pachytragus* species have the same size and proportions despite the smaller overall size of *P. crassicornis*. *Megalovis latifrons* has a slightly shorter premolar row than does *Palaeoryx pallasi*.

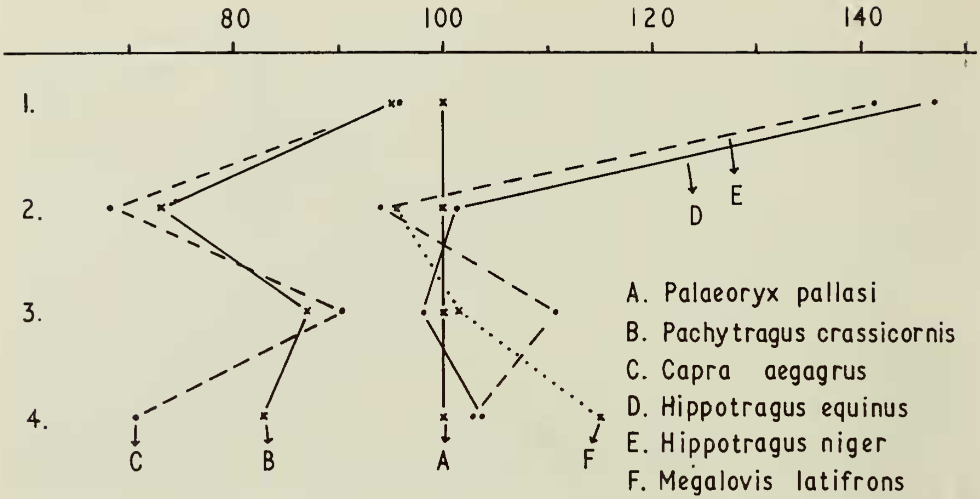

FIG. 10. Percentage diagram to compare some mean skull measurements of *Palaeoryx pallasi* (the standard line at 100%) and *Pachytragus crassicornis* with males of some living Bovidae: *Capra aegagrus* (10 individuals), *Hippotragus equinus* (10), and *H. niger* (12). Three measurements of *Megalovis latifrons* from Senèze are also shown, based on only one reading for separation of horn cores and two for the other two measurements. The measurements numbered 1 to 4 on the left of the diagram are the same as in Text-fig. 1. *Capra aegagrus* may differ from *Pachytragus crassicornis* by its more closely inserted but large horn cores, and has small teeth. The two *Hippotragus* species are rather more different from *Pachytragus crassicornis*, *H. niger* being slightly smaller but with larger horn cores.

Dentitions

The teeth which Schlosser (1904, pl. 11 figs 2, 4, 5) put in *Pachytragus crassicornis* may be taken as *Pachytragus* of some species although those of figs 2 and 5 are rather scrappy, but the teeth of pl. 11 figs 1 and 3 which he also placed in *P. crassicornis* are more likely to be of *Miotragocerus*. The teeth of pl. 8 figs 1 and 2 assigned to *Palaeoryx stützeli* are also of *Miotragocerus*.

COMPARISONS. Teilhard de Chardin and Trassaert (1938 : 41) described from the lower or perhaps later Pliocene of China an antelope called ?*Protoryx yushensis* which from the figures appears to match *Pachytragus crassicornis* in its short braincase widening anteriorly in dorsal view, and keels on the horn cores. The horn cores are rather short (as in Lausanne skull remains 30 and 31). In anterior view the horn cores diverge more than in the Samos skulls. The Chinese skull may well be a closely related species.

Of the two Samos species of *Pachytragus* it is *P. laticeps* which must be the more primitive on the basis of horn cores without anterior keels, the orbital rims being only moderately wide alongside the horn core insertions, and the less developed median occipital ridge and its poorer flanking hollows.

III. SYSTEMATICS OF SPIRAL HORNED ANTELOPES

Clearly spiralled horns occur among living antelopes as follows.

Tragelaphini	all species	Africa	horns in males only, except in *Taurotragus* and one species of *Tragelaphus*
Hippotragini	*Addax nasomaculatus*	Sahara desert	horns in both sexes
Antilopini	*Antilope cervicapra*	India	horns in males only
Caprini	*Capra caucasica*	Caucasus	horns in both sexes
	C. falconeri	India	horns in both sexes
	Ammotragus lervia	North Africa	horns in both sexes
	Pseudois nayaur	Central Asia	horns in both sexes
	Ovis ammon	Eurasia	horns sometimes in males only, but many populations with horned females as well
	O. canadensis	Siberia, N. America	horns in both sexes

It is apparent that several independent evolutions of spiralled horns have taken place.

The first fossil antelope with spiral horn cores to be described was *Antilope lindermayeri* from Pikermi by Wagner (1848 : 367), later transferred by Gaudry (1865 : 290) to *Palaeoreas*. Wagner (1857 : 154) described another spiral horned antelope from Pikermi, *Antilope rothi*, which Gaillard (1902 : 93) took as the type species for his genus *Oioceros*. Pikermi had two more spiral horned antelopes to yield, both of them already present in Gaudry's material assigned to *Palaeoreas lindermayeri*. These were *Protragelaphus skouzesi* Dames (1883 : 97) and *Helicoceras rotundicornis* Weithofer (1888 : 288) the latter's generic name subsequently becoming *Helicotragus*.

As the only species of its genus, *Palaeoreas lindermayeri* has had a simple history. Gaudry (1861) named the genus in accordance with his belief that it was an early tragelaphine, and since then it has not been moved from that tribe. *Prostrepsiceros* has had a more complicated history. Major (1891a : 609) took as his genotype the species *Tragelaphus*? *houtumschindleri* then newly described by Rodler & Weithofer (1890 : 768) from Maragha. He referred Samos specimens to a new species *P. woodwardi* and to *Prostrepsiceros*? sp. Schlosser (1904 : 31) named a similar specimen from Samos *Protragelaphus zitteli*, considering it closely related to Dames's *P. skouzesi*. Pilgrim & Hopwood (1928 : 84, 89, 91) regarded Major's *Prostrepsiceros woodwardi* as a *nomen nudum* and themselves assigned to it a holotype. They added a third species, *P. mecquenemi*, to the genus for Mecquenem's (1924 : 37) Maragha material in Paris, which he had assigned to *P. houtumschindleri*. They assigned *Protragelaphus zitteli* Schlosser to a new genus, *Hemistrepsiceros*, and in this species they also placed Major's *Prostrepsiceros*? sp.

Ozansoy (1965) referred some Turkish fossils to new species of *Palaeoreas* and *Helicotragus*, but they come from later Plaisancian deposits than other species of those genera, and it is difficult to relate them convincingly to the older species.

Prostrepsiceros and *Hemistrepsiceros* have been regarded as members of the Tragelaphini, but Pilgrim & Hopwood (1928 : 20) assigned *Helicotragus* to the Antilopini, and Pilgrim (1939 : 129, 135) thought that *Protragelaphus skouzesi* should go there as well. The purpose of the second part of this paper is to transfer *Prostrepsiceros* to the Antilopini and *Palaeoreas* to the Ovibovini, and to revise the Samos, Pikermi and Maragha species of these genera. I shall also discuss *Protragelaphus skouzesi* which I accept as an antilopine. I have already briefly referred to these questions (Gentry 1968 : 874).

The two genera *Prostrepsiceros* and *Protragelaphus* share the following skull characters, which can be taken as a kernel for defining any suprageneric grouping to which they and their relatives may belong. They have an open spiralling of the horn core or a twisting of its axis which is anticlockwise from the base upwards on the right side, no transverse ridges on the horn cores nor a flattened lateral surface, little divergence of the horn cores, complicated mid-frontals and parieto-frontal sutures, temporal lines wide apart on the top of the braincase, braincase sides parallel or widening slightly posteriorly in dorsal view, a preorbital fossa, a moderate area of exposure of the mastoid, the ventral edge of the auditory bulla not descending posteriorly to meet the front of the paraoccipital process, fairly hypsodont cheek teeth, and quite short premolar rows.

Although both genera are known at Pikermi and Samos, it is the more complete remains in the Paris collection from Maragha which are the most important for their interpretation.

Genus ***PROSTREPSICEROS*** Major

1891a *Prostrepsiceros* Major : 609.
1903 *Helicotragus* Palmer : 873.
1928 *Hemistrepsiceros* Pilgrim & Hopwood : 94.

Type species. *Tragelaphus*? *houtumschindleri* Rodler & Weithofer.

Generic diagnosis. Small to moderate sized antelopes; horn cores are moderately long, with keels or traces of keels, no deep longitudinal grooving, inserted above the orbits and rather obliquely in side view, moderately wide apart at their insertions in anterior view and rather openly spiralled; postcornual groove is fairly shallow or moderately deep; frontals are not hollowed internally.

Orbital rims project; frontals between horn bases are only marginally higher than orbital rims; supraorbital pits are moderate-sized; preorbital fossa is moderate to large.

Nuchal crests are poor to moderate; median vertical occipital ridge and flanking hollows are poor to moderate; anterior tuberosities on the basioccipital are moderately sized with some development of longitudinal ridges behind them; anterior tuberosities are close together, hence a central longitudinal groove is seen anteriorly; auditory bulla is large and inflated.

Teeth are known from only one of the two contained species.

Prostrepsiceros houtumschindleri (Rodler & Weithofer)

1890 *Tragelaphus? houtum-schindleri* Rodler & Weithofer : 768, pl. 6 fig. 2.
1891a *Prostrepsiceros woodwardi* [nom. nud.] Major : 608.
1891a *Prostrepsiceros* sp. Major : 608.
1904 *Protragelaphus zitteli* Schlosser : 31, pl. 6 figs 2, 3, 5, 12.
1924 *Tragelaphus houtum schindleri* Mecquenem : 37, pl. 5 figs 5, 7; pl. 6 figs 5, 7.
1928 *Prostrepsiceros woodwardi* Pilgrim & Hopwood : 91, pl. 7 figs 1, 1a, 1b.
1928 *Prostrepsiceros mecquenemi* Pilgrim & Hopwood : 92.
1928 *Hemistrepsiceros zitteli* (Schlosser). Pilgrim & Hopwood : 94.

HOLOTYPE. A frontlet from Maragha in the Natural History Museum, Vienna, numbered 1886.XXVIII.6.

LOCALITIES. Samos and Maragha.

AGE. Lower Pliocene.

DIAGNOSIS. Horn cores are robust, with some latero-medial compression, medial surface less convex than lateral one (Maragha), strong posterior keel descending to a postero-lateral insertion or posterior keel absent, another keel descending to an anterior or antero-medial insertion and strong in those without a posterior keel, and poor to moderate divergence; braincase is strongly angled on the face.

The remaining characters are known in Maragha specimens only: nasals are fairly long with transverse doming and small lateral and central flanges anteriorly; ethmoidal fissure is moderate-sized and narrow; premaxillae rise with even width and have a short contact on the nasals.

Teeth are fairly hypsodont; basal pillars are absent on upper molars but sometimes present on lowers; there are no indentations into back edges of rear central cavities of upper molars; medial lobes of upper molars do not join to one another and to lateral side of tooth until quite late after eruption; styles and ribs on upper molars are poor; lower molars have goat folds; P_4 has a medial opening between paraconid and metaconid; metaconid of P_4 is directed backwards; lateral wall of P_4 is indented in front of the hypoconid.

REMARKS. *Material from Maragha. P. houtumschindleri* is represented in Vienna by the damaged type frontlet with left horn core, a left horn core 1886.XXVIII.9, and two other horn cores, 1886.XXVIII.8, from Maragha. There are many Maragha specimens in Paris including the skull figured by Mecquenem (1925, pl. 5 fig. 5 for its teeth and pl. 6 fig. 7) which lacks the distal parts of its horn cores and the braincase, a second skull also lacking its braincase (Pl. 5 fig. 1), a skull with M^2 and M^3 on both sides but lacking the left side and back of the braincase and the face above the tooth row, a cranium with right horn core on which the front of the basioccipital is missing, and many other dentitions and horn cores.

The original illustration of this species by Rodler and Weithofer (1890, pl. 6 fig. 2) was probably constructed from both the type frontlet and the better preserved left horn core, 1886.XXVIII.9. The divergence of the horn cores on the holotype exceeds that on most of the Paris examples, although the Paris specimen with the most completely preserved cranium does have a similarly pronounced divergence.

A second variety from Samos

From Samos there is a skull BM(NH) M.4192 (Pl. 5 fig. 3), a frontlet with left horn core, M.4210, and part of a right horn core, M.4213; a frontlet with horn cores from Brown's quarry 6, AMNH 20575 and a left horn core from quarry 5, AMNH 20576; a frontlet figured by Schlosser (1904, pl. 6 fig. 5) in Munich; and a frontlet, 1911 Samos V 130, in Vienna. Schlosser's specimen does not have so compressed a section in its upper parts as the others, and shows that any tendency to a posterior keel is confined to near the horn core tip. In these Samos examples which have hitherto been placed in the species *woodwardi* and *zitteli*, the horn cores have an anterior keel but no posterior keel. They are a distinct variety from the Maragha specimens, but I take them as conspecific by their robust, little divergent, keeled horn cores and by the braincase top being so angled on the face axis.

Dentitions

The two mandibles figured as *P. houtumschindleri* by Mecquenem (1924, pl. 5 fig. 7 and pl. 6 fig. 5) agree in size with the upper dentitions attached to skulls. They show small back lobes on the M_3s, very small or absent basal pillars on the molars of one and moderate to small basal pillars on the other, goat folds on the molars, the anterior part of the medial wall of P_4 is not closed, metaconid of P_4 is directed backwards, the lateral wall of P_4 is indented just in front of the hypoconid, and the horizontal ramus is not very deep. Large numbers of lower partial dentitions of this size are present in the Maragha collections in Paris, and even though some may belong to other species it is very likely that many belong to the same species as the most numerous horn core type. The most likely alternative identity for some of these mandibles is *Oioceros rothi*, which is present at Maragha but less numerous than *Prostrepsiceros houtumschindleri*. The only indication of the size of the teeth in this species is provided by the skull of Mecquenem (1924, pl. 7 fig. 7). It is not certain that this skull is of *O. rothi*, but by its basioccipital morphology it is certainly not a *Prostrepsiceros*. Its tooth row (Mecquenem pl. 6 fig. 4) is slightly smaller than those of the skulls of *P. houtumschindleri*, but suggests that there would be a considerable size overlap between dentitions of the two species. There is no perceptible morphological variation among the mandibles of this size range as they are preserved, and it would not be surprising if *O. rothi* had very similar teeth to *P. houtumschindleri*.

The supposed *P. rotundicornis* mandible from Maragha (Mecquenem 1924, pl. 7 fig. 5) is smaller than the mandibles among which some may be accepted as *P. houtumschindleri*, its molars have no goat folds, the basal pillars range in size from moderate on M_1 and M_2 to slightly smaller on M_3, and the back lobe of M_3 is quite large and possesses a central cavity. This and other similar mandibles are not *P. houtumschindleri*, but they might belong to the species which Mecquenem (1924 : 30) called *Gazella deperdita* (see p. 284 footnote and Gentry 1970 : 273).

The specific name of this species was wrongly spelled by Pilgrim & Hopwood (1928) as *houtum-schlindleri* with two 'l's.

Prostrepsiceros rotundicornis (Weithofer)

1865 *Palaeoreas lindermayeri* (in part) Gaudry : 292, pl. 52 fig. 5.
1888 *Helicoceras rotundicorne* Weithofer : 288, pl. 18 figs 1–4.
1889 *Helicophora rotundicornis* (Weit.). Weithofer : 79.
1903 *Helicotragus rotundicornis* (Weit.). Palmer : 873.
1908 *Antidorcas? gaudryi* Mecquenem : 52.
1924 *Helicophora rotundicornis* Mecquenem : 39, pl. 7 fig. 1.
1926 *Helicoceras fraasii* Andree : 163, pl. 11 fig. 4; pl. 15 fig. 1.
1928 *Helicotragus fraasii* (Andree). Pilgrim & Hopwood : 23.

LECTOTYPE. The Pikermi specimen figured by Weithofer (1888, pl. 18 figs 1, 2) in the Natural History Museum at Vienna was chosen by Pilgrim & Hopwood (1928 : 21).

LOCALITIES. Pikermi, Samos, Maragha.

AGE. Lower Pliocene.

DIAGNOSIS. Horn cores are less massive than in Maragha examples of *P. houtumschindleri*, with some degree of antero-posterior compression; posterior keel

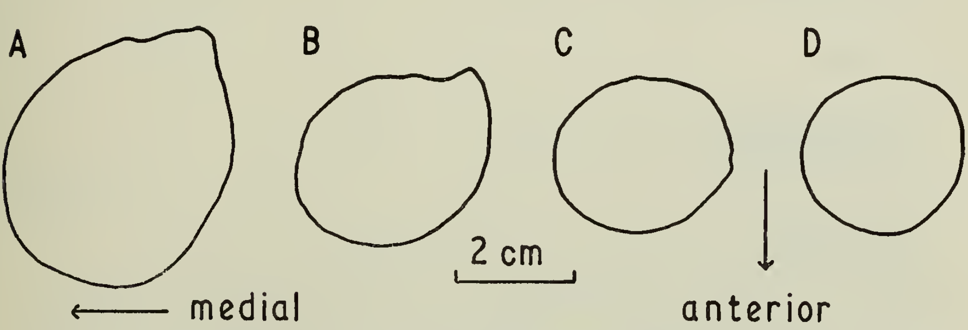

FIG. 11. Sections of left horn cores from Maragha taken at a distance above the pedicel top equal to half the antero-posterior diameter at the base of the horn core. A = *Protragelaphus skouzesi* (Mecquenem 1924, pl. 6 fig. 6); B = *Prostrepsiceros houtumschindleri* (Mecquenem 1924, pl. 6 fig. 7); C = *P. rotundicornis* (Mecquenem 1924, pl. 7 fig. 1); D = *Antilope cervicapra*, BM(NH) 32.12.11.8.

is absent; a trace of an anterior keel is present and descends to an antero-medial or medial insertion; braincase is not strongly angled on the axis of the face.

Remarks. *The Pikermi variety.* The last species existed in two well marked varieties at Maragha and Samos but was absent from Pikermi; this one also exists in two clear varieties, but one occurs at both Maragha and Samos, and the other at Pikermi. *P. rotundicornis* is less completely preserved than *P. houtumschindleri* but the following specimens are known. In London there is the Pikermi material listed by Pilgrim & Hopwood (1928 : 23), among which the incomplete skull M.11437 was figured by them (pl. 1 figs 2, 2a). There are also horn cores from Pikermi in Paris. The Pikermi material shows not very great divergence of the horn cores, not exceeding that of most of the *P. houtumschindleri* material, the horn cores are inserted rather obliquely at the base, and the basal part of the horn core before any outward swing begins is short. The skull M.11437 has a trace of a posterior keel at its base.

A second variety from Maragha and Samos

Maragha examples of this species are represented possibly by two single horn cores numbered 1886.XXVIII.8 in Vienna and by many specimens in Paris among which the more important are the frontlet figured by Mecquenem (1924, pl. 7 fig. 1), a cranium with the left horn core and part of the left preorbital fossa (Pl. 5 fig. 2), two further frontlets, and a frontlet possessing only the left horn core. The Maragha specimens of this species have horn cores inserted more uprightly, and a long basal part followed by a strong outward swing. It is interesting that there is a cranium with horn cores from Samos which agrees with the Maragha variety of *P. rotundicornis*.

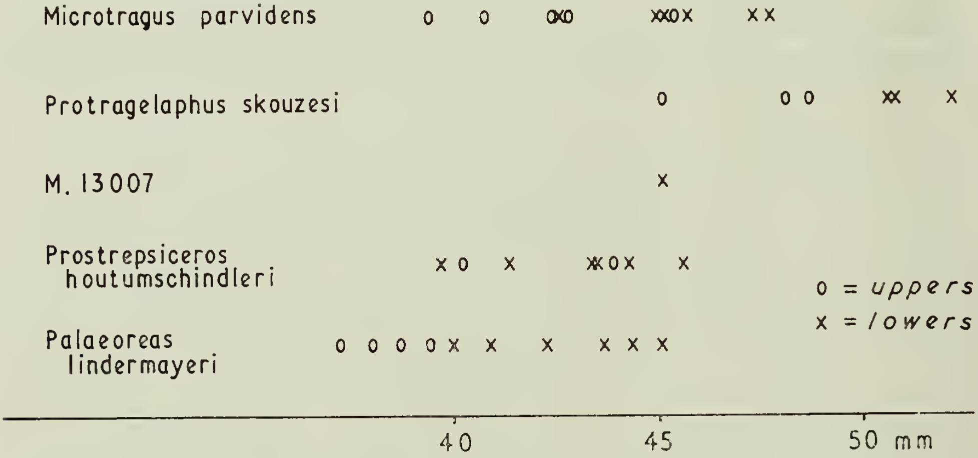

Fig. 12. Lengths of upper and lower molar rows of some antelopes. The uppers are from identified skulls only; the lowers of *Palaeoreas lindermayeri* and *Protragelaphus skouzesi* are fairly easily recognizable; the *Sporadotragus* (=*Microtragus*) *parvidens* is only doubtfully identified. The *Prostrepsiceros houtumschindleri* is from Maragha only, and the *Palaeoreas lindermayeri* from Pikermi only.

It was figured by Andree (1926, pl. 11 fig. 4 and pl. 15 fig. 1), and I have seen at Münster a cast of the original specimen kept at Stuttgart. The horn core on the left side is sufficiently near complete to show that its divergence as a whole does not exceed that in other *Prostrepsiceros* despite the outward swing above the basal part. The braincase of this specimen appears to be angled on the face rather more than in the Pikermi M.11437 or in the Maragha specimen figured here, but it is less angled than in *P. houtumschindleri*.

Major (1894 : 25) listed two Samos horn cores in Lausanne, 204 and 205, as *Helicophora rotundicornis*, but I believe that they are more likely to belong to *Oioceros wegneri* Andree (1926 : 170, pl. 15 figs 3, 6).

The Pikermi examples of this species are the ones which have been called *rotundicornis* in the past, while the Maragha ones and the Samos example have been called *fraasi*.

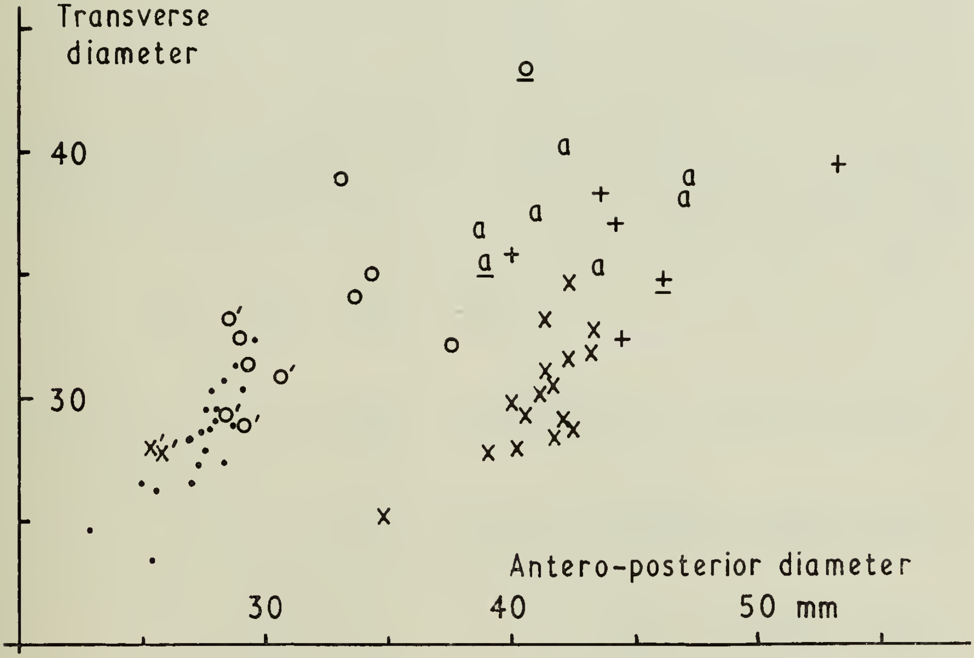

FIG. 13. Graph of horn core compression. x = *Prostrepsiceros houtumschindleri* from Maragha, x′ = *P. houtumschindleri* from Samos, o = *P. rotundicornis* from Maragha, o′ = *P. rotundicornis* from Pikermi, + = *Protragelaphus skouzesi*, a = *Palaeoreas lindermayeri* (including a̲ the Samos specimen in Lausanne), · = *Antilope cervicapra*. o̲ and ± are the casts in Münster of *Prostrepsiceros rotundicornis* and *Protragelaphus skouzesi* from Samos. The Samos *Prostrepsiceros houtumschindleri* and the Pikermi *P. rotundicornis* are closest to *Antilope* but the Maragha *P. rotundicornis* is rather larger. *Protragelaphus skouzesi* and Maragha *Prostrepsiceros houtumschindleri* are more medio-laterally compressed than the others.

Both varieties of *P. rotundicornis* differ from *P. houtumschindleri* by less massively built horn cores, keels absent or nearly absent, an 'anterior' keel in so far as one is ever present perhaps descends to a medial rather than to an antero-medial insertion, the horn cores are not more compressed higher up than lower down, the braincase is less angled on the face axis (Pl. 5 fig. 2), and the supraorbital pits are perhaps smaller.

On the percentage diagram (Text-fig. 14) *Prostrepsiceros rotundicornis* from both Pikermi and Maragha has horn cores more like those of *Antilope cervicapra* than has the Maragha *P. houtumschindleri*; the horn cores of the Pikermi *P. rotundicornis* are also small enough to approach the size of those of *Antilope cervicapra*.

Dentitions

The only example of a mandible I have been able to find which might belong to this species is BM(NH) M.13007, a left mandible from Pikermi with P_3 to M_3 in an early stage of wear (Pl. 6 fig. 2). It had been assigned to *Palaeoreas lindermayeri* (Pilgrim & Hopwood 1928 : 87). There is a small back lobe of M_3; basal pillars are of small to moderate size on M_1, small on M_2 and absent on M_3; there are goat folds on the molars; the metaconid of P_4 is directed backwards and there is quite a deep indentation on the lateral wall in front of the hypoconid. All these characters cause M.13007 to resemble the slightly smaller *Prostrepsiceros houtumschindleri* mandibles from Maragha, but the ramus may be slightly deeper below the tooth row. The teeth are slightly larger than in a number of *Palaeoreas lindermayeri* mandibles from Pikermi, the molars have larger goat folds, and P_3 is relatively

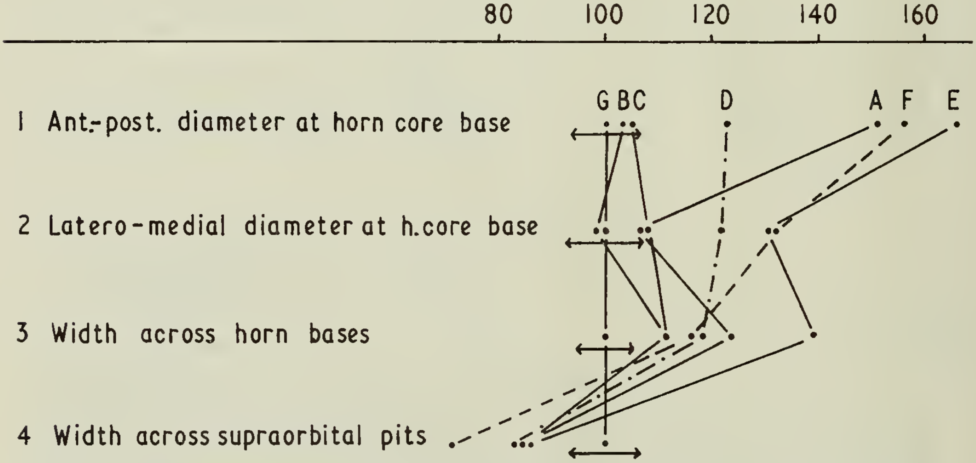

Fig. 14. Percentage diagram for some skull measurements of spiral-horned antelopes, based on Table 3 in the text. The standard line at 100% is the mean of 20 male *Antilope cervicapra*, and means of the other species are expressed as percentages of their values in *A. cervicapra*. Horizontal lines show the extent of standard deviations in *A. cervicapra*. The capital letters, A to G, indicate the species concerned as on Table 3, p. 274.

smaller. The complete premolar row would have been relatively longer than in *Protragelaphus skouzesi*, which in any case has larger teeth. M.13007 is not small enough to belong to a gazelle or probably to *Oioceros rothi* (see discussion on p. 264), but it would be the right size for *Sporadotragus parvidens*. Other mandibles which I have tentatively assigned to *S. parvidens* in my notes, e.g. BM(NH) M.13009, M.13011 and M.4184; AMNH 22778 and 86415, differ only in less or no development of goat folds, so M.13007 cannot be definitely taken as *Prostrepsiceros rotundicornis*. My expectation would have been to find a smaller tooth row in this last species. The right M_1 and M_2 of an immature Samos antelope illustrated by Schlosser (1904, pl. 13 fig. 12), agree with M.13007.

Genus ***PROTRAGELAPHUS*** Dames

1883 *Protragelaphus* Dames : 97.

Type species. *Protragelaphus skouzesi* Dames.

Generic diagnosis. As for the species, which is the only one in the genus.

Protragelaphus skouzesi Dames

1857 *Antilope lindermayeri* (in part) Wagner : 155, pl. 7 fig. 18.
1865 *Palaeoreas lindermayeri* (in part) Gaudry : 291, pl. 53 fig. 4.
1883 *Protragelaphus skouzesi* Dames : 97.

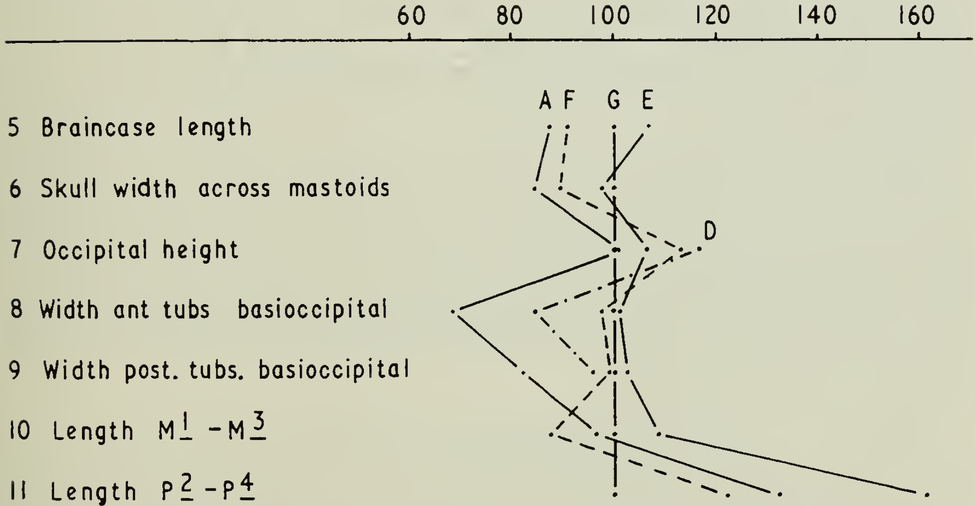

Fig. 15. Percentage diagram for further skull measurements of spiral-horned antelopes. Explanation under Text-fig. 14. The braincase length was measured from the mid-frontals' suture at the level of the supraorbital pits to the occipital top. Standard deviations for *Antilope cervicapra* could not be shown on this diagram, and have been listed after Table 3 in the text, p. 275.

Holotype. The Berlin frontlet described but not figured by Dames. Pilgrim & Hopwood (1928 : 88) take Wagner's figure as being of the paratype. Gaudry's figure is a right mandible which is the size of this species, and was so taken by Pilgrim & Hopwood.

Localities. Pikermi, Samos and Maragha.

Age. Lower Pliocene.

Diagnosis. Moderate sized antelopes (larger than *Prostrepsiceros*); skull is fairly low and wide; horn cores are long, not medio-laterally compressed but the posterior keel adds to the antero-posterior diameter, with a strong posterior keel descending to a postero-lateral insertion but no anterior keel, inserted a little behind the orbits and rather obliquely in side view, inserted moderately wide apart in anterior view, moderately diverging, and the axis itself is twisted and lacks the open spiralling of *Prostrepsiceros*; postcornual fossa is usually moderate or large sized; frontals are hollowed; orbital rims slope rather than project strongly; braincase top is short and strongly angled on face axis; frontals are slightly higher between the horn bases than the level of the orbital rims; frontals surface is convex in front of the horn bases; mid-frontals suture may be raised; parieto-frontals suture is indented; supraorbital pits are smaller than in *Prostrepsiceros* and moderately wide apart; nasals are fairly long; suture at back of nasals is narrowly drawn out as a V-shape; preorbital fossa is moderate to large sized; infraorbital foramen is above the front half of P^3; premaxillae may rise with an even width to a short contact with the nasals; median palatal indentation is level with or behind lateral ones; nuchal crests are poor to moderate; occipital surface is more nearly in one plane facing backwards than in *Prostrepsiceros*; median occipital ridge and flanking hollows are poorly marked; anterior tuberosities of the basioccipital are wider apart than in *Prostrepsiceros*; anterior tuberosities are small with poor longitudinal ridges behind.

Teeth are fairly hypsodont; the enamel is only slightly rugose; basal pillars are very small on upper molars and small to moderate on the lowers, decreasing backwards; rear central cavities of upper molars have indented back edges; medial lobes of upper molars remain unfused to one another fairly late in wear; styles and ribs are poor; goat folds on lower molars are poor or non-existent; premolar row is short; metaconid of P_4 may join the paraconid and close the anterior part of the medial wall; the lateral wall of P_4 is indented in front of the hypoconid; P_3 is shorter relative to P_4 than in *Palaeoreas*.

Remarks. The more important fossils of *Protragelaphus skouzesi* which I have seen are the paratype skull from Pikermi in Munich, two skulls in Paris from Maragha one of which was figured by Mecquenem (1924, pl. 6 fig. 6 and pl. 5 fig. 2), a cranium in London, M.10840, from Pikermi, a frontlet from Samos in Stuttgart, and a fontlet from Maragha in Vienna. There are other Maragha horn cores in Paris. I have not seen the holotype, nor the cranium in Göttingen figured by Weithofer (1888, pl. 17 figs 4–6).

The Stuttgart specimen figured by Andree (1926, pl. 15 figs 4, 5) is the only decisive evidence for this species from Samos; I did not see the original but was able to see a plaster cast in Münster. The twisting of the keels on this Samos specimen is rather tight and the keel stronger than in other specimens; at its base the keel connects by a ridge with the back of the orbit. The London cranium has the back part of the braincase stuck to the front, and it is possible that the braincase appears to slope too little on the face axis on this specimen.

There is a palate from Maragha in Paris which seems to belong to this species, and in addition I would assign to it these dentitions and teeth: mandibular pieces BM(NH) M.13021 and M.13022 (Pl. 6 fig. 2) from Pikermi, AMNH 86478 from Samos, 618 and 661 from Samos in Lausanne, and the Paris mandible figured by Mecquenem (1924, pl. 6 fig. 1) from Maragha. These pieces show that the teeth of this species are large among the smaller antelopes of lower Pliocene times but smaller than the common Samos genus *Pachytragus*.

COMPARISONS. *Protragelaphus skouzesi* differs from *Prostrepsiceros* as a whole by its greater size; more posterior horn insertions; a twisting of the horn core axis rather than an open spiralling; the combination of strong posterior keel on the horn cores and no anterior keel is not found in any known *Prostrepsiceros* population (Text-fig. 11); higher frontals between the horn bases; hollowed frontals with a convex surface in front of the horn bases; orbital rims projecting little; smaller supraorbital pits; occipital surface more definitely in one backwardly-facing plane; and wider anterior tuberosities on the basioccipital with less of a longitudinal central groove between them.

It differs additionally from *P. houtumschindleri* in not having any medio-lateral compression of its horn cores (Text-fig. 13); a narrowly drawn out suture at the back of its nasals; upper molars with spurs often projecting into the back edges of the rear central cavities; no goat folds on its lower molars; and a tendency for paraconid-metaconid fusion to close the anterior part of the medial wall of P_4. The Maragha mandible figured by Mecquenem (1924, pl. 6 fig. 1) has a completely fused paraconid and metaconid on its P_4. It differs additionally from *P. rotundicornis* by its braincase being more strongly angled on the facial axis, and by the horn cores being more obliquely inserted than in Maragha and Samos specimens.

On the percentage diagram (Text-figs 14 and 15) *Protragelaphus skouzesi* is quite similar to the smaller *Prostrepsiceros houtumschindleri*, the latter having relatively narrower anterior tuberosities of its basioccipital. One can visualize the common ancestor of this pair not too far in the past.

Genus **PALAEOREAS** Gaudry

1861a *Palaeoreas* Gaudry : 299.
1861b *Palaeoreas* Gaudry : 395.

TYPE SPECIES. *Antilope lindermayeri* Wagner.

GENERIC DIAGNOSIS. There is only one species within the genus, so the generic diagnosis is as for that species.

Palaeoreas lindermayeri (Wagner)

1848 *Antilope lindermayeri* Wagner : 367, pl. 12 fig. 5.
1861a *Palaeoreas lindermayeri* Gaudry : 299.
1861b *Palaeoreas lindermayeri* Gaudry : 395.
1865 *Palaeoreas lindermayeri* Gaudry : 290, pl. 52 fig. 4; pl. 53 figs 1–3; pl. 54; pl. 55.

HOLOTYPE. Base of a right horn core in the Palaeontological Institute, Munich, no. 530. The antero-posterior diameter at the base of this horn core is 42·1 and the latero-medial diameter 40·2 mm.

LOCALITIES. Pikermi and Samos.

AGE. Lower Pliocene.

DIAGNOSIS. Small to moderate sized antelopes; horn cores are moderately long and massive (more massive than in *Prostrepsiceros houtumschindleri*), not mediolaterally compressed, often with deep fairly irregular longitudinal grooving, with a posterior keel which is sometimes strong and a weaker anterior keel, the posterior keel descending to a postero-lateral position, horn cores inserted above the orbits, set fairly obliquely in side view, close together in anterior view and poorly divergent, and the axis itself twisted anticlockwise from the base up on the right side but without open spiralling; there is an elongated very deep postcornual fossa. Orbital rims project moderately; mid-frontals and parieto-frontals sutures are not visible; temporal lines on braincase roof probably do not approach closely posteriorly; braincase may widen posteriorly; large supraorbital pits; mid-frontals suture is raised as an incipient ridge in front of the horn bases; there is another localized raising of the mid-frontals suture behind the horn bases; the ethmoidal fissure is long and narrow; preorbital fossa is extensive and moderately deep; face is low in side view; infraorbital foramen is above the back part of P^2; the premaxillae rise with an even width to a short contact on the nasals.

Occipital surface is low and its dorsal edge is not evenly rounded; the median vertical occipital ridge is strong with large shallow flanking hollows; mastoids are moderate to large; basioccipital is long with a central longitudinal groove weaker in the centre than at either end; nuchal crests are moderately strong; auditory bulla is inflated and moderate to large, and its ventral edge does not descend posteriorly to meet the front of the paraoccipital process.

The teeth are fairly hypsodont (but perhaps less than in *Prostrepsiceros* and *Protragelaphus*); basal pillars are small or absent on the upper molars and slightly larger on the lowers; there are not usually indentations in the back edge of the rear central cavities on the upper molars; medial lobes of the upper molars remain unfused with one another until fairly late in wear; styles on upper molars are moderate sized and a rib between parastyle and mesostyle is often fairly strong; there is a tendency to goat folds on the lower molars; front and back edges of P_3 and P_4 are set transversely: anterior medial wall of P_4 is not closed; the metaconid on P_4 is not directed backwards; there is no valley in front of the hypoconid on the lateral wall of P_4; P_3 has a strong entostylid behind the entoconid; and P_3 is fairly large in relation to P_4.

REMARKS. There is a face with horn cores M.10843, several frontlets, and many horn cores of this species in London, all Pikermi. There are three skulls, and many other horn cores from Pikermi in the Paris collection. Three frontlets, 23, 24 and 25 (Pl. 6 fig. 1) in Lausanne are the only known occurrence of the species from Samos. In the London collection I assign the following mandibular pieces to this species: the four numbered M.11505, M.13008, M.13012, M.15828 (Pl. 6 fig. 2) and M.15829. Pilgrim & Hopwood (1928 : 23, 70) had assigned M.11505 and M.13012 differently, but they did have M.13008 as *P. lindermayeri*. Of the other dentitions which they assigned to *P. lindermayeri*, I believe M.13007 has a P_3 too small in relation to P_4 for assignation to *Palaeoreas lindermayeri* (see p. 268), and the others I would not care to identify.

In the Paris collection from Pikermi is a fine small palate with M^1–M^3 measuring 39·4 mm long, M^2 13·9 mm, and P^2–P^4 28·3 mm long. The rear median indentation passes further forwards than the lateral ones, ribs are strong between parastyle and mesostyle on the molars, M^1 alone has a very small basal pillar, and the medial lobes of the molars are still not joined to the lateral sides of the teeth. I have taken this as *P. lindermayeri*, as it agrees with other dentitions on the Paris and London skulls in its strong ribs.

The species is thus very common at Pikermi, but rare at Samos. It has been recorded from other sites, but I would not accept most of these records based as they are on doubtful dentitions. However Schlosser (1921 : 44) recorded a horn core from Veles in Macedonia. It is principally from the London skull and the series of more or less complete ones in Paris that the diagnosis has been constructed. It is unfortunate that some weathering or rolling has taken place on these skulls, so that the details of structure are often missing. On one of the two Paris skulls in which they are present the nasals are transversely domed and on the other they are not. Nor could I be certain about the level of the median indentation at the back of the palate.

The Samos skull in Münster which was named *Oioceros wegneri* by Andree (1926 : 170, pl. 15 figs 3, 6) has many resemblances to *Palaeoreas lindermayeri*, for example no horn core compression, deep longitudinal grooving on the horn cores, the great height of the frontals between the horn bases, a localized raising of the mid-frontals suture anterior to the horn bases, and a long narrow ethmoidal fissure. Such similarities are surprising when it is realized that the torsion of the horn cores is in the reverse direction from *P. lindermayeri*. The only other clear differences of *O. wegneri* from *P. lindermayeri* are that the torsion is stronger, the spiralling more open, the keel descends to a lateral insertion, and the braincase is shorter with a more steeply inclined roof. I have considered *Oioceros* as quite unrelated to *Palaeoreas*, *Protragelaphus* or *Prostrepsiceros*.

COMPARISONS. *Palaeoreas lindermayeri* is the most distinctive of the lower Pliocene spiral horned antelopes. It differs from *Prostrepsiceros* and *Protragelaphus* by its more massive horn cores, horn cores sometimes with deep irregular longitudinal grooving, a stronger posterior keel than in all except the Maragha *P. houtumschindleri*, horn cores not very compressed antero-posteriorly or medio-laterally (Text-fig. 13), a deeper postcornual fossa, braincase more strongly bent on the face axis, frontals higher between the horn bases, the mid-frontals and parieto-frontals sutures not visible, larger supraorbital pits closer together, perhaps a larger ethmoidal fissure, stronger median vertical occipital ridge and thus more of a tendency for the occipital surface to face partly laterally as well as posteriorly, perhaps a slightly larger mastoid, basioccipital larger, basioccipital with less localized anterior tuberosities and as large a central longitudinal groove as the strongest ones in *P. houtumschindleri*, and probably a stronger rib between parastyle and mesostyle on the upper molars.

TABLE 3

	A	B	C	D	E	F	G
Antero-posterior diameter at base of horn core	41·3 (11)	28·3 (3)	28·6 (3)	33·5 (5)	45·4 (5)	42·7 (7)	27·3 (20)
Latero-medial diameter at base of horn core	30·3 (11)	27·8 (2)	30·5 (3)	34·5 (5)	37·1 (5)	37·3 (5)	28·3 (20)
Minimum width across lateral edges of horn pedicels	92·2 (9)	82·9 (3)	82·7 (3)	87·9 (3)	103·7 (5)	86·5 (5)	74·4 (20)
Width across lateral edges of supraorbital pits	40·2 (8)	40·3 (2)	40·4 (2)	39·4 (3)	41·7 (4)	34·0 (5)	47·6 (19)
Braincase length from level of supraorbital pits to occiput	89·9 (1)	—	—	—	109·4 (1)	93·5 (4)	102·4 (20)
Skull width across mastoids behind exterior auditory meatus	69·0 (1)	—	—	—	79·8 (2)	73·3 (4)	81·7 (17)
Occipital height from top of foramen magnum	27·1 (1)	—	—	31·3 (1)	28·7 (2)	30·5 (6)	26·9 (19)
Width across anterior tuberosities of basioccipital	15·5 (1)	—	—	19·2 (1)	22·8 (3)	22·2 (4)	22·7 (17)
Width across posterior tuberosities of basioccipital	23·8 (1)	—	—	27·8 (1)	29·7 (2)	28·9 (4)	29·0 (15)
Length M^1–M^3	42·0 (2)	—	—	—	47·3 (2)	38·3 (4)	43·6 (16)
Length P^2–P^4	27·2 (1)	—	—	—	33·2 (1)	25·2 (3)	20·6 (12)

A = *Prostrepsiceros houtumschindleri* from Maragha only.
B = ,, ,, from Samos only.
C = ,, *rotundicornis* from Pikermi only.
D = ,, ,, from Maragha only.
E = *Protragelaphus skouzesi* from Pikermi and Maragha.
F = *Palaeoreas lindermayeri* from Pikermi only.
G = *Antilope cervicapra*, males of the living blackbuck.

It differs additionally from *Prostrepsiceros* by its horn cores with a twisted axis instead of more open spiralling and perhaps by smaller auditory bullae, and from *P. houtumschindleri* by less strong goat folds on its lower molars, transversely set front and back edges of P_3 and P_4, the metaconid on P_4 is not directed backwards, no indentation on the lateral wall of P_4 in front of the hypoconid, a larger P_3 and P_3 with a strong entostylid. It differs additionally from *Protragelaphus skouzesi* by less divergent horn cores, more projecting orbital rims, the back of the nasals less narrowly drawn out, the transverse front and back edges of P_3 and P_4, no closing of the anterior part of the medial wall of P_4, no indentation on the lateral wall of P_4 anterior to the hypoconid, the large size and strong entostylid of P_3.

On the percentage diagram (Text-figs 14 and 15) *Palaeoreas lindermayeri* has large horn cores and a fairly large back part of the skull (characters 5–9 inclusive) compared with the size of the tooth row; the massiveness of the back of the skull presumably being linked with the size of the horn cores.

Table 3 shows the means of some skull measurements of spiral horned antelopes used in Text-figs. 14 and 15 and the figures in brackets are the size of the sample. Standard deviations for the sample of *Antilope cervicapra*, listed in the same order as the measurements, are: 1·78, 2·21, 4·14, 3·27, 3·46, 3·85, 2·26, 1·82, 1·67, 2·26 and 1·34.

IV. TRIBAL CLASSIFICATION

The Palaeoryx, Protoryx and Pachytragus group

Comparison with Hippotragini

The tribe Hippotragini includes the following living species:

Hippotragus equinus (Desmarest 1804) the roan,
Hippotragus niger (Harris 1838) the sable antelope,
Oryx gazella (Linnaeus 1758) the gemsbok and beisa,
Oryx dammah (Cretzschmar 1826) the scimitar oryx,
Oryx leucoryx (Pallas 1777) the Arabian oryx,
Addax nasomaculatus (Blainville 1816) the addax.

They are medium to large-sized stocky antelopes with large horn cores in both sexes, hypsodont cheek teeth with basal pillars on the molars, and little reduction of premolars. *Hippotragus* has a long braincase and medio-laterally compressed horn cores strongly curved backwards, *Oryx* has a shorter braincase and little-compressed straight horn cores, and *Addax* has a shorter braincase and spiralled horn cores.

The older authors gave but few reasons why they regarded *Palaeoryx*, *Protoryx* and *Pachytragus* as Hippotragini. Gaudry (1861a : 241; 1861b : 394) in writing of *Palaeoryx* mentions the form, proportions and insertion of the horn cores, position of the supraorbital pits and lack of wide orbital rims as resembling modern *Oryx*, although its teeth were certainly very different. Major (1891a : 608) in founding

Protoryx writes of a more decided hippotragine aspect than even *Palaeoryx* possessed —horn cores bigger relative to skull size, brachyodont teeth, and in some species a short parietal. The reference to brachyodonty as a resemblance is puzzling. Apart from that, it seems that the little compressed and obliquely inserted horn cores of *Palaeoryx* cause it to resemble *Oryx*, and that *Protoryx* with its more compressed and uprightly inserted horn cores can be regarded as not unlike *Hippotragus*.

So far this is not very convincing, and the only other resemblances of the fossils to Hippotragini lie in characters which can reasonably be supposed to be primitive. Thus the fossils have no keels on the horn cores (except in *Pachytragus crassicornis*), the extent to which the frontals are raised between the horn bases is about the same, there are no transverse ridges on the front of the horn cores, the horns are inserted above the back of the orbits, the horn cores of *Protoryx carolinae* and *Pachytragus laticeps* diverge about as much as in *Hippotragus*, the horn cores have a simple course without torsion, postcornual fossae are small or absent, the orbital rims have about the same width, the supraorbital pits are small, an ethmoidal fissure is present, the infraorbital foramen above the tooth row is in about the same position, the palatal foramina are at about the same antero-posterior level, the mastoids are large, the anterior tuberosities of the basioccipital are set about as widely apart, and the degree of hypsodonty in *Pachytragus* approaches that of Hippotragini.

Two other possible resemblances to the Hippotragini need further discussion; these are the solid horn cores of the fossils and the dimensions of their braincases. The fossil horn cores are mostly solid, but traces of a basal hollowing have been found (see p. 248). Hippotragini also have solid horn cores, but in them the central lowest parts are at most only slightly spongy in texture, and I have found no sign of the development of hollowing. A collection in Cape Town of the large extinct *Hippotragus gigas* Leakey from the Elandsfontein Pleistocene site confirms this. Hollowing of the frontals extends to the top of the horn pedicels, above which the horn core itself is not hollowed. A very large East African frontlet of the same species in Nairobi (figured by Leakey 1965, pls 89, 90) has the frontal hollowing extending about 35 mm above the external indication of the pedicel top, but this hollowing is clearly demarcated from the horn core substance above. A male roan antelope in the National Museum, Nairobi was sectioned 20 mm above the top of its horn pedicel and at that level it was solid. So the hollowing in the fossil AMNH 23038 (see p. 249) already exceeds that in *Hippotragus*, and even the extreme sponginess of AMNH 22783 would not be expected in *Hippotragus*. It is therefore difficult to derive the totally solid condition of living *Hippotragus* from that of the fossils in which hollowing has already been initiated.

Braincase lengths of the fossils can be matched with one or other of the Hippotragini. Thus *Palaeoryx pallasi* agrees with *Oryx*, *Protoryx carolinae* and longer-brained *Pachytragus* with *Hippotragus equinus*, and other *Pachytragus* with *Hippotragus niger*. This is in line with the supposed connection of *Palaeoryx* with *Oryx*, and of *Protoryx* and *Pachytragus* with *Hippotragus*. However the resemblance ends here. The bending down of the braincase on the facial axis is less in either species of *Hippotragus* than in *Protoryx* and *Pachytragus*, and braincases of *Hippo-*

tragus are wider than in the fossils. With the differences in inclination and proportion, it is difficult to see that the length of the braincases can indicate any real connection of the fossils with Hippotragini.

Turning to the differences of the fossils from Hippotragini, we find that the most important ones concern the teeth. Hippotragini retain basal pillars on their molars, and have strong outbowed labial ribs between the styles on their upper molars. *Hippotragus* itself has evolved large basal pillars, complicated central cavities on its upper molars, goat folds on its lower molars, and relatively large premolars (Text-fig. 5). It is obvious that the teeth of the two *Pachytragus* species are not evolving in this direction. Even if one could discuss a possible hippotragine relationship for *Palaeoryx* or *Protoryx*, one could certainly not do so for *Pachytragus*.

Finally in comparing the Samos fossils with modern Hippotragini, one should mention that there are two fossil hippotragines from the Pinjor stage of the Siwalik Hills in India and Pakistan (perhaps of early Pleistocene age) which are substantially different from living Hippotragini but do not suggest a derivation from *Protoryx* or *Pachytragus*. These two fossils are *Sivatragus bohlini* (Pilgrim 1939 : 80, pl. 2 figs 3–6, text-fig. 6) and *Sivoryx sivalensis* (=*Antilope sivalensis* of Lydekker 1878 : 154, pl. 25 figs 1, 2) which I take to include *S. cautleyi* (Pilgrim 1939 : 74); both are represented in the British Museum (Natural History). Neither have the frontals between the horn bases raised above the level of the orbital rims; *Sivatragus bohlini* shows boselaphine-like characters in the braincase being little angled on the line of the (absent) face and in its fairly marked temporal lines behind the horn bases, and is further unlike the Samos and Pikermi antelopes in its braincase being definitely wider posteriorly than anteriorly; *Sivoryx sivalensis* has rather a low and wide skull and its upper molar teeth have basal pillars and are without such marked mesostyles as *Pachytragus*. Derivation of *S. sivalensis* from *Palaeoryx pallasi* could not be ruled out on morphological grounds, but *P. pallasi* is too large to be a likely ancestor.

I conclude from all the above evidence that *Palaeoryx*, *Protoryx* and *Pachytragus* cannot be placed in the Hippotragini.

Comparison with the Caprini

Most of the primitive skull characters in which the fossils resemble Hippotragini are also resemblances to Caprini, and particularly to goats (*Capra* Linnaeus 1758) within the Caprini. Caprini are wholly Palaearctic except only for *Capra walie* Rueppell 1835 which has reached a part of the Ethiopian highlands and *Ovis canadensis* Shaw 1804 which has spread into America.[2] If the Samos antelopes should turn out to be caprines, the supposed African affinities of that fauna would be much diminished. It is therefore of interest to look for further caprine resemblances in the fossils.

The delimitation of the species of goats and their very near relatives (*Capra*,

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[2] *Oreamnos americanus* (Blainville 1816), the Rocky Mountain goat, is also in North America, but Simpson (1945 : 162) places *Oreamnos* in the tribe Rupicaprini of the subfamily Caprinae.

Hemitragus, Ammotragus, Pseudois) adopted by Ellerman and Morrison-Scott (1951 : 403–410) and the arrangements of more recent authors are clearly unsatisfactory in their various ways. Many of the named forms can interbreed to produce fertile offspring (Gray 1954 : 70), and striking differences of male horns probably have little taxonomic value. This has been Payne's (1968) point of view, and although I do not follow him to all his conclusions, it seems unlikely that we could find separate ancestors for most or all of the 'species' of *Capra* very far back in the geological record. In this paper I shall use the specific names of Ellerman and Morrison-Scott within the genera *Hemitragus, Ammotragus* and *Pseudois*, and within *Capra* the following names: *C. aegagrus* Erxleben 1777 for goats with an anterior keel on their horn cores, *C. ibex* Linnaeus 1758 for the European ibex, *C. sibirica* (Pallas 1776) for Siberian ibexes, *C. caucasica* Güldenstaedt & Pallas 1783 for the Caucasian turs, and *C. falconeri* (Wagner 1839) for the spirally horned markhors.

There are a number of characters in which the Samos fossils, especially *Pachytragus*, are similar to goats, and taken together these characters indicate convincingly a relationship of the fossils to goats. These characters are as follows.

An anterior keel exists on the horn cores of *Pachytragus crassicornis*, the most advanced of the fossils, and on those of *Capra* and *Hemitragus*. In AMNH 22938 and AMNH 22939 the keel descends to an antero-medial insertion; this would allow for the later development of an antero-lateral longitudinal swelling such as can be seen in many *Capra aegagrus*. The beginning of such a swelling may be present in AMNH 20708. This swelling could so easily develop into the broad anterior surface of ibex horn cores, that one doubts whether ibexes necessarily had different ancestors from *C. aegagrus* as far back as the lower Pliocene.

The cranium AMNH 23037 of *Pachytragus laticeps* has horn cores completely preserved to their tips, and in profile their course is not an even arc with a large radius of curvature like *Hippotragus* but they become more sharply curved towards their tips; such a curvature resembles that in the male horns of living goats and ibexes. Other examples of *Pachytragus* fail to show this so well, but it does occur in the *Pachytragus laticeps* cranium 201 in Lausanne, and in AMNH 20674 and 20690.

Extensively hollowed horn cores are characteristic of the living Bovini and Caprini, but in other bovid tribes hollowing is confined to the frontals and horn pedicels. Traces of hollowing near the bases of the horn cores have been noted in *Pachytragus* (page 248), and this would be appropriate in ancestors or relatives of later Caprini.

The bending down of the braincase on the axis of the face in *Protoryx* and *Pachytragus* is a character also found in goats.

In some *Pachytragus* (and *Palaeoryx*) individuals a tendency exists for the widest part of the braincase to lie anteriorly. It appears in the Lausanne skull 30 which is probably a *Pachytragus laticeps*, in the Münster skull of *P. crassicornis* figured by Andree (1926, pl. 13 fig. 7), in a number of the New York *Pachytragus* skulls, and in the *Pachytragus* skull from Salonica figured by Arambourg & Piveteau (1929, pl. 7 figs 6, 6a). It can also be seen in the *Palaeoryx pallasi* skull BM(NH) M.10831 and in the Munich example of the same species from Samos, but two other *P. pallasi* braincases widen posteriorly. In Hippotragini the sides of the braincase are either parallel or widen posteriorly, but in living Caprini they are parallel or widen anteriorly.

On Text-fig. 4 it can be seen that the supraorbital foramina have become wider apart, relative to the distance across the horn bases, in *Pachytragus crassicornis* than in *P. laticeps*, and this character would link *P. crassicornis* more closely with *Capra*.

The ethmoidal fissure is not only present in both species of *Pachytragus*, but is also long and narrow as in *Capra*, *Hemitragus* and *Ammotragus*; it is less wide than in Hippotragini.

The *Pachytragus* face of AMNH 20609 has a jugal which is not unlike that of *Capra*, but is without the two unequally-sized lobes of a *Hippotragus*. It does not show any antero-ventral expansion and smoothly rounded overall course of the front suture like many individuals of caprine species.

The foramina ovalia are small to moderately sized in the fossils as in Caprini instead of moderate to large as in Hippotragini.

In the type skull and in the cranium AMNH 20621 of *Pachytragus laticeps* and in the Lausanne cranium 29 (Pl. 1 fig. 1) and Münster cranium (Andree 1926, pl. 13 figs 4, 6) of *Palaeoryx pallasi*, the auditory bullae have survived, and it can be seen that the posterior part of their ventral edges turn downwards to meet the front of the paraoccipital processes as in the caprines *Hemitragus*, *Pseudois*, *Ammotragus* and many *Capra*. I took this to be a resemblance of the fossils to Caprini (Gentry 1968 : 874), and although this was correct I have since found that the character occurs frequently in the sable antelope.

The diminution of basal pillars on the cheek teeth of *Pachytragus laticeps* and *P. crassicornis* foreshadows their almost total absence in the teeth of living Caprini; the central cavities of the upper molars have an uncomplicated outline; in *P. laticeps* and *crassicornis* the mesostyle is frequently prominent on the upper molars and is followed by a concave lateral wall behind as in Caprini. Finally the short premolar row (Text-fig. 9, already shorter in *P. laticeps* and *P. crassicornis* than in *Hippotragus*) and somewhat reduced P^2 in the fossils foreshadow later Caprini. Such teeth can convincingly be seen as an intermediate stage in the evolution of modern caprine teeth from the fairly generalized original condition of bovid teeth such as is seen in *Palaeoryx pallasi* and *Protoryx carolinae*.

An extremely interesting character to know would be the size of the central incisor teeth in *Palaeoryx*, *Protoryx* and *Pachytragus*, for they are small in all Caprini (as in most Eurasiatic antelopes) but larger in Hippotragini (as in most African antelopes). The mandible AMNH 23073 had I_1s perhaps only slightly bigger than the more lateral incisors and canine like Caprini, but clear evidence from an unworn dentition is required. A mandibular symphysis in Münster of an unknown Samos antelope of the size of *Pachytragus* has rather small I_1s.

Text-fig. 10 shows the relative proportions of some skull measurements in the fossils and living antelopes. The sable antelope has larger horn cores than the roan and both have rather long braincases, the last character being exaggerated on the diagram because of the relative shortness of the braincase in *Palaeoryx pallasi*, here used as a standard. *Capra* and *Pachytragus crassicornis* have similar proportions of the cranium, but *Capra* has very large horn cores and small teeth.

It is difficult to interpret the evolutionary history of *Pachytragus*, not least because of the lack of precise details about the vertical distribution of its species. It is known only that *P. crassicornis* in the New York collection is confined to Brown's quarry 5, while quarries 1 and 4 contain the less advanced *P. laticeps*. The supposition that quarry 5 might be later than the other quarries depends on the morphological interpretation of the two species of *Pachytragus*; Sondaar (1968 : 68) has mentioned a time difference between the quarries but without specifying whether quarry 5 was the later. Except for the relative smallness of the teeth in *Capra*, there seems no reason why *Pachytragus crassicornis* should not be the actual ancestor of goats. A more detailed knowledge of later Pliocene faunas is desirable before asserting this more definitely.

Tossunnoria pseudibex Bohlin (1937 : 37, pl. 4 fig. 3, pl. 5 figs 1–3, text-figs 66–68, 70b, 71–74), a caprine from the lower Pliocene of north eastern Tibet, has been linked with the ancestry of goats. It has large very strongly compressed horn cores inserted at a high angle to one another so that their bases diverge backwards. Its braincase widens posteriorly. I am prepared to relate it to *Pachytragus* among its contemporaries, and very tentatively to *Hemitragus* among its successors. Its horn cores are more advanced or specialized than in *Pachytragus*.

Differences of the Samos fossils from living Caprini

A number of advanced characters of later Caprini are absent in the lower Pliocene fossils: the extreme enlarging of male horn cores and the linked raising of the level of the frontals between the horn bases, the frequently posterior setting of the palatal foramina, and the very wide anterior tuberosities of the basioccipital. The primitive state of these characters in the fossils were previously noted as similarities to Hippotragini; such resemblances may simply result from the acquisition of some specializations in Caprini later than the earlier Pliocene. Other later caprine characters not met with in these fossils are the very wide projection of the lower rim of the orbits (less pronounced in *Ovis ammon* and *Ammotragus lervia* than in other living Caprini), the tendency to antero-ventral expansion of the jugal and an evenly curved course of its front suture which is most apparent in *Pseudois*, *Ammotragus* and *Hemitragus*, the small angle of the lower jaw, the fusion of the metaconid and paraconid on P_4, the presence of goat folds on lower molars, and high transverse crests across little worn and unworn upper molars. The crests across the upper molars are detectable on dentine as well as enamel and must result from rigidly fixed transverse occlusal movements. Possible initial traces of such wear are visible on the *Pachytragus laticeps* and *P. crassicornis* specimens in Münster figured by Andree (1926, pl. 12 fig. 2 and pl. 13 fig. 7).

Among these characters by which modern goats differ from *Pachytragus*, the large horn cores with extensive hollowings, raised frontals, and wide basioccipital suggest that the method of intraspecific fighting used by *Capra* (see Schaffer 1968) had not yet evolved. It may be mentioned that although the sparse and inadequately identified antelope limb bones from Samos have not been studied in this paper, there are no extremely shortened goat-like metapodials in any museum collection to suggest that even *Pachytragus crassicornis* had entered areas of precipitous rocky slopes.

If we consider other skull characters than those in which the fossils are less advanced than all living genera of Caprini, we find that *Pachytragus* is still not very close to *Ovis*, the latter genus differing strongly in its broad-fronted divergent curled horn cores and no ethmoidal fissure.[3] *Pseudois* differs by its non-compressed divergent horn cores often with deep longitudinal grooving in mature animals, the short braincase very strongly angled on the face, the generally advanced outline of the jugal, no preorbital fossa or ethmoidal fissure, and small mastoid. *Ammotragus* differs by its non-compressed divergent horn cores, the generally advanced outline of its jugal, no preorbital fossa and no ethmoidal fissure. *Hemitragus* differs by its short horn cores, long dorsal parts of its orbital rims, often an expanded jugal, and no preorbital fossa. *Capra aegagrus* differs in the absence of a preorbital fossa, and it is this form from which *Pachytragus*, especially *P. crassicornis*, is least remote; *Capra falconeri* has a large posterior keel and strongly twisted horn cores, most ibexes have broad-fronted horn cores (the prominent knobs on the sheaths are not present on the cores), and *Capra caucasica* has horn cores rather more reminiscent of *Ammotragus* or *Pseudois*.

The position of Palaeoryx pallasi

The similarities noted between the Samos fossils and living goats have principally concerned *Pachytragus* and especially *P. crassicornis*. Little positive sign of a connection between *Palaeoryx pallasi* and goats can be seen. Although *P. pallasi* cannot satisfactorily be taken as in the Caprini, it does have some similarities to later members of other tribes of Caprinae, for example the living East Asian *Capricornis* Ogilby. The resemblance to *Capricornis* is at least as great as to the hippotragine *Oryx*. More interesting are its similarities to *Megalovis latifrons* from the Villafranchian of Senèze, France (Schaub 1923 : 292, fig. 5; 1943 : 281, figs 5 and 6). Some fossils assigned to *Pliotragus* (=*Deperetia*) *ardeus* are very probably conspecific with *M. latifrons*, e.g. the cranium illustrated by Schaub (1923, fig. 3) and the skull from the Villafranchian of Olténie in Romania illustrated by Bolomey (1965, figs 1–3). It is even possible that this species includes the original maxilla of *Antilope ardea* Depéret (1884, pl. 8 fig. 3) in which case nomenclatorial alteration

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[3] It may be more difficult in the future to determine the ancestry of sheep than of goats. *Sivacapra* Pilgrim (1939 : 49) from the Pinjor stage of the Siwaliks has torsion of its horn cores which is clockwise on the right side and it is a possible relative of sheep. It has resemblances both to *Sinotragus* mentioned on p. 243 above and to *Samotragus crassicornis* Sickenberg (1936) from Samos, which in its turn is like *Oioceros wegneri* Andree (1926 : 170, pl. 15 figs 3, 6). Yet it is impossible to link *Sinotragus* with *Oioceros* if the former's relationship to *Protoryx* and *Palaeoryx* (p. 243) is accepted, so one is faced with two caprine stocks having clockwise torsion of their horn cores. The assignation of individual fossils becomes difficult, and we also have to find out whether sheep descend from either stock or from some other form such as *Sporadotragus* (see p. 283 below).

of *M. latifrons* to *M. ardea* would be needed. Villalta & Crusafont Pairo's (1955 : 431, figs 1–3) *Hesperoceras merlae* from Villaroya must be at least a close relative of *M. latifrons*. Bolomey's skull in particular suggests a connection with *Palaeoryx pallasi*, with which it shares or from which it could easily have derived the following characters: large size (both species are large among their contemporaries), short to moderately long horn cores, little compression of the horn cores (Text-fig. 8), horn cores strongly divergent and inserted behind the level of the orbits, braincase angled on the axis of the face, short braincase, small supraorbital pits set widely apart, and the back of the tooth row lying just anteriorly to the level of the front of the orbits. Text-fig. 10 shows that a couple of measurable *Megalovis latifrons* have rather larger horn cores and tooth rows than in *Palaeoryx pallasi*. Other Villafranchian skull pieces I examined in Paris and Basle show further characters in common with *Palaeoryx pallasi*: not very complicated mid-frontals and parieto-frontals sutures, a large mastoid, and a wide basioccipital. However, the teeth of these Pleistocene fossils are more advanced than in *P. pallasi*, and the relative length of the premolar row a little reduced (Text-fig. 9).

Accepting *Pachytragus* as a definite member of the Caprini, one can either place *Palaeoryx* and *Protoryx* with it as close relatives or separate them, placing *Palaeoryx* in the same tribe as *Megalovis*. The correct tribal position for *Megalovis* has been a problem, some authors relating it to sheep and others to the Ovibovini (Guérin 1965 : 12). Unlike Schaub (1923) I take it as an ovibovine. It agrees with the Ovibovini (discussed further on page 289) or at least with the living *Ovibos* and *Budorcas* in its large size, dorso-ventral compression of the horn cores, their insertion behind the orbits and very wide divergence, presence of a ridge from the base of the horn core to the top back of the orbit, short braincase, well projecting orbital rims, not a complicated mid-frontals suture, small supraorbital pits which are set widely apart, infraorbital foramen placed as far posteriorly as above the back of P^3, an indication of concavities postero-laterally to the anterior tuberosities of the basioccipital, small auditory bulla, absence of basal pillars on the molar teeth, upper molars rather long relative to width, upper molars with fairly strong styles and rounded medial lobes, P^2 remaining large, mandible not markedly deep below the molars, and paraconid of P_4 fused to the metaconid. In addition the quite sharp upstanding ridges on the posterior tuberosities of the basioccipital and the central longitudinal groove constricted between the anterior tuberosities are like *Budorcas*. There seems to be no reason to link *Megalovis* with sheep which have horn cores inserted above the orbits, emerging without much divergence, and with a marked spiral course. I suggest that *Megalovis* is an ovibovine and that *Palaeoryx* too be placed in that tribe. This opinion is tentative, and I have not seen the *Megalovis* skull from Olténie, but I believe it is better to have a definite and possibly interim classification than one with an unworkable proportion of queried assignations. In the same manner I shall take *Protoryx* and its Asian relatives as Caprini, although there is hardly any balance of probabilities taking them closer to that tribe than to Ovibovini. With *Palaeoryx* no longer related to *Oryx*, the evidence for rather dry steppe conditions at Pikermi, if not also at Samos, is diminished. An ancestor of *Oryx* could be visualized with a tendency to inhabit the rather dry areas favoured by the living species, but we do not know what habitats might have held an ancestor of *Megalovis latifrons*.

Other related lower Pliocene fossils

The foregoing revision has been concerned only with species of *Palaeoryx*, *Protoryx* and *Pachytragus* occurring at Samos, Pikermi and Maragha. *Paraprotoryx*, *Prosinotragus*, *Sinotragus* and *Sinoryx* have been mentioned in the comparisons, and there are other Eurasian Pliocene bovids which should probably be removed from the Hippotragini, namely *Pseudotragus*, *Leptotragus*, *Olonbulukia* and *Sporadotragus*.

Pseudotragus capricornis founded by Schlosser (1904 : 51) on Samos material is represented by the type skull in Munich (Schlosser 1904, pl. 10 fig. 7) by a poorly preserved skull in New York (AMNH 20577), by the London skull BM(NH) M.4193, and by some dentitions in Munich (Schlosser 1904, pl. 10 figs 1–3, 5, 6). The Munich examples are in a different matrix from the other bovids (Schlosser 1904 : 112–113), hence there is a good likelihood that the teeth are correctly referred; the New York specimen is from Brown's quarry 6 in which, like quarry 2, *Pachytragus* is not represented. *Leptotragus* was founded by Bohlin (1936 : 8, figs 2, 3) for a second smaller skull referred by Schlosser (1904 : 51, pl. 10 fig. 8) to *Pseudotragus capricornis*, the supposed generic difference being based on its straighter and narrower horn cores, larger orbits situated more anteriorly, horn cores set more obliquely and having an anterior keel. It seems unlikely that *Leptotragus pseudotragoides* can be separated specifically from *Pseudotragus capricornis*, but I was not able to check the specimen in Munich which was probably destroyed in the Second World War. *Pseudotragus* in Schlosser's original sense is smaller than *Pachytragus*, and has relatively very large, strongly compressed horn cores, well projecting orbital rims, a long premolar row and a relatively large P^2. It resembles Caprini in the rather small size of the face relative to the cranium and in the braincase being strongly angled on the face.

Olonbulukia tsaidamensis Bohlin (1937 : 30, pl. 2 figs 10, 11, pl. 3 fig. 1) is based on a cranium from the supposed lower Pliocene of Tsaidam in China. It is about the size of *Pachytragus* or *Pseudotragus*, has horn cores strongly compressed lateromedially, with an anterior keel, little divergent and curved backwards in side view. There is a postcornual fossa and the braincase would have been somewhat angled on the missing face. *Olonbulukia* shows no clear sign of tribal affinities in itself, but it can continue to be tentatively taken as an Asian relative of *Pachytragus* and *Protoryx*.

Sporadotragus Kretzoi (1968) is the corrected name for *Microtragus* Andree (see p. 234). It is again smaller than *Protoryx*. It differs from *Pseudotragus* by having less compressed horn cores, frontals very strongly raised between the horn bases, horn cores frequently with an anterior surface, and narrower orbital rims. The middle two of the preceding characters, along with the rather small face (Pikermi) and widening of the anterior parts of the braincase (Pikermi) are decidedly caprine-like and the clear upper and lower rims of the preorbital fossa recall sheep in particular.

I suggest that *Pseudotragus* (including *Leptotragus*) and *Sporadotragus* be transferred to the Caprini, while *Olonbulukia* be regarded as ?Caprini.

The skull of *Tragoreas oryxoides* Schlosser (1904 : 34, pl. 6 figs 1 and 9) is from a small antelope with strongly compressed and obliquely inserted horn cores, frontals less raised between the horn bases than in *Pseudotragus*, no upraised mid-frontals suture, a preorbital fossa without an upper rim, a fairly large P^2, and an apparently undistorted brain top which is scarcely angled on the face axis. It could be related to *Miotragocerus* on the basis of these characters, although smaller than the smallest species of that genus, *M. valenciennesi* Gaudry (1865 : 288). No feature of its morphology suggests membership of the Hippotragini, but only the strongly compressed horn core would go against such an assignation. Doubtful placing in the Boselaphini seems a better solution to the problem, since it would not be satisfactory to use this unique and puzzling specimen as the only basis for the presence of Hippotragini at Samos.[4]

Ancestors for the Palaeoryx group

Nothing certain is known of the ancestors of *Palaeoryx, Protoryx* or *Pachytragus*. Earlier representatives of the boselaphine genus *Miotragocerus* than the Samos, Pikermi and Maragha species are known from the Sarmatian of the Vienna Basin (Thenius 1959 : 87) and the Chinji of India and Pakistan, and the related genera *Protragocerus* and *Eotragus* also occur at such early time levels. But the record for pre-Pannonian Caprini includes only *Oioceros* from Tung Gur, Fort Ternan and Prebreza, ?*Pseudotragus potwaricus* (Pilgrim) from the Siwaliks and Fort Ternan and its possible relative ?*Gazella stehlini* from Europe. (See Gentry (1970) for discussion and references to these occurrences.) The only bovid which is a possible candidate for ancestry of *Palaeoryx, Protoryx* or *Pachytragus* is *Damalavus boroccoi*, known as a cranium and other horn cores and teeth from the Miocene of Oued Hammam (=Bou Hanifia) in Algeria. It was described by Arambourg (1959 : 120,

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[4] Bohlin (1935c : 107, pl. 13 figs 7–14, pl. 14 figs 1–6) described two fine skulls of *Tragoreas lagreli* from the Chinese lower Pliocene which he later suggested should be renamed *T. altidens* (Bohlin 1941 : 107). They had somewhat compressed horn cores set very closely together, very deep postcornual fossae, the front of the braincase at a high level relative to the face, but the back part bent downwards. Should *Tragoreas* become unavailable as a generic assignation for this species, it could be referred to *Pseudotragus* or to *Dorcadoryx* Teilhard de Chardin & Trassaert (1938 : 32), possibly as a separate species from their *D. triquetricornis*. A number of horn cores in the Paris collection from Maragha may be close to '*Tragoreas*' *altidens*; they are short and thick, there is a very deep postcornual fossa, wide orbital rims, and a braincase much angled on the face. A frontlet has been illustrated (Mecquenem 1924, pl. 3 fig. 3), and all of the Maragha specimens are larger than the *Gazella deperdita* from the type locality, Mount Léberon, to which they were referred. (Another Maragha frontlet of this supposed gazelle in Vienna had previously been named by Rodler & Weithofer (1890 : 767, pl. 5 fig. 1 and pl. 6 fig. 1) as *Gazella capricornis*, changed to *G. rodleri* by Pilgrim & Hopwood (1928 : 16), and later said by Pilgrim (1939 : 45) to be possibly an *Oioceros*. In the absence of well marked torsion of its horn cores there is no reason to assign it to *Oioceros*.) A frontlet from the Nagri stage of the Siwalik Hills in Pakistan which Pilgrim (1939 : 86, pl. 2 figs 1, 2) called gen. indet. (cf. *Tragoreas*) *potwaricus* and the same species from the Fort Ternan upper Miocene in Kenya are unlikely to be linked with *Tragoreas oryxoides* or with '*Tragoreas*' *altidens*; I have written elsewhere that a relationship to *Pseudotragus* is just possible (Gentry 1970 : 288).

pl. 18 figs 4, 4a) as an alcelaphine, and the type specimen does resemble a *Damaliscus*, but with a long braincase and short more obliquely inserted horn cores. It is alternatively possible that this ancient antelope could be an ancestor of *Palaeoryx* (this may have been Arambourg's (1954 : 297) first opinion of it when he wrote of a *Palaeoryx* at the site). It is large for its geological age but smaller than *P. pallasi*, the horn cores are only moderately long, slightly curved backwards and obliquely inserted in side view, without keels and with perhaps a slight lessening of divergence towards their tips. The cranium has been transversely crushed, as Arambourg noted; its horn cores may have been slightly more divergent in anterior view, and their insertions a little wider than actually appears. There is a shallow postcornual fossa, small supraorbital pits, the frontals between the horn bases are hardly higher than the orbital rims, the braincase is moderately long and not very strongly bent on the face axis (this is a difference from *Palaeoryx*, but one which is probable in its putative ancestor), mid-frontals and fronto-parietal sutures are fairly complicated, and there are no temporal ridges—only temporal lines which do not approach very closely posteriorly. This absence of temporal ridges might remove it from candidature for boselaphine ancestry. Measurements on this specimen, comparable with those taken on *Palaeoryx* and *Protoryx* are: antero-posterior and transverse diameter of horn core 40·2 and 32·8 mm.

A left M_3 which Monsieur Arambourg showed me in Paris appeared to be a companion piece to the right M_3 assigned to *Tragocerus* (now *Miotragocerus*) and shown in pl. 17 figs 4, 4a of his work and was of a size to go with *Damalavus*. It was 22·0 mm long at its occlusal surface, and the height of its medial wall between front and central lobes was 10·2 mm.

As to the age of Oued Hammam, Arambourg (1959 : 10) thought it was Tortonian. Cooke (1968 : 249) believed it could be later, and I agree (Gentry 1970 : 312). It would be of much zoogeographical interest if the affinities of *Damalavus* could be definitely decided, but I was unable to do this when I saw the material in Paris.

Spiral horned antelopes

Comparison with Tragelaphini

Prostrepsiceros and *Palaeoreas* have always been taken as Tragelaphini although Pilgrim (1939 : 129, 135) moved *Protragelaphus* to the Antilopini. The living Tragelaphini are a fairly homogeneous group of browsing African antelopes found in habitats ranging from montane moorlands to forest but generally where there is at least some bush. They are mostly large sized. Their skulls have keeled and spiralled horn cores with anticlockwise torsion on the right side, which is their major resemblance to the Eurasian Pliocene fossils. Otherwise they show quite a distinctive pattern of skull characters which is not at all foreshadowed in the fossils. These are that a postcornual fossa is absent, horn cores tend to insert behind the orbits, the dorsal part of the orbital rims slopes from the horn bases and projects very little, the frontals between the horn bases are a little raised above the level of the orbital rims, the mid-frontals and parieto-frontal sutures disappear in adult males, the braincase sometimes widens posteriorly, a perforation in the side of the braincase is often seen behind the postorbital bar, the orbital surface of the lachrymal is at a wide angle to its facial surface, the supraorbital foramina are in lengthened narrow pits, a preorbital fossa is absent, the infraorbital foramen is placed anteriorly and rather low, the premaxillae narrow anteriorly to a blunt point, the occipital surface has a flat top edge and straight sides, the mastoids are small, the basioccipital is long with anterior tuberosities in front of the foramina ovalia and it has a transverse constriction centrally, and P_4 often has a fused paraconid and metaconid.

Tragelaphini retain as probably primitive characters a braincase which is little angled on the face axis, long nasals, an ethmoidal fissure, brachyodont cheek teeth, medial lobes of the upper molars which do not fuse with one another until late in wear, lower molars without goat folds, and long premolar rows with large front premolars. The extinct *Tragelaphus nakuae* Arambourg (1941 : 343; 1947 : 418) from Omo in southern Ethiopia is appreciably more primitive than living tragelaphines in its projecting orbital rims, supraorbital pits not elongated antero-posteriorly, and an occipital surface which is perhaps less squared in outline.

The resemblances of *Prostrepsiceros*, *Protragelaphus* and *Palaeoreas* to Tragelaphini lie almost entirely in primitive characters, and none of them are evolving towards the sort of morphology seen in living tragelaphines. Sometimes they may show resemblances, as for example in the long basioccipital of *Palaeoreas lindermayeri*, but such resemblances are few and apparently fortuitous. In the past Tragelaphini have been linked with the Boselaphini and Bovini, which is a position I support (Gentry 1970 : 316), and it would certainly be awkward to accommodate in the same overall group the small spiral horned genera from Samos.

Comparison with the Indian blackbuck

I would rather put *Prostrepsiceros* and *Protragelaphus* into the same group as the living Indian blackbuck, *Antilope cervicapra* (Linnaeus 1758). Whereas Tragelaphini tend to be larger antelopes, the blackbuck is a fairly small bovid like most of the fossils. This and its lack of the specialized features of Tragelaphini make it quite a strong contender for relationship to the fossils. Its fairly long horn cores, their spiralling with anticlockwise torsion on the right side, their inclination in side view, width across the insertions and the amount of divergence are all about the same as in *Prostrepsiceros* and *Protragelaphus*.

It agrees with both the *Prostrepsiceros* species in its horn cores being inserted above the orbits, frontals not being raised between the level of the horn bases, and in the moderate projection of the orbital rims, but these characters amount only to a lack of the more specialized conditions found in *Protragelaphus*. Going down to species level, one finds that some facial and dental characters of *P. houtumschindleri* agree with *A. cervicapra*. The small central and lateral flanges anteriorly on the nasals (Pl. 5 fig. 1) and the premaxillae rising with even width to a contact on the nasals give *P. houtumschindleri* quite a striking resemblance to the blackbuck. The near absence of basal pillars on the molars (complete absence in the blackbuck), poor styles and ribs on the upper molars, lower molars with goat folds (slightly less marked in the blackbuck), no paraconid-metaconid fusion on P_4, and the indented lateral wall of P_4 in front of the hypoconid are additional resemblances. It is quite possible that such resemblances would also be found in the unknown face and dentition of *P. rotundicornis*. With *P. rotundicornis* in particular the blackbuck agrees in the absence of keels, no medio-lateral compression of its horn cores, and the poor degree of bending of the braincase on the face axis.

Antilope cervicapra is practically devoid of keels and this obviously gives it more resemblance to *P. rotundicornis* than to any other of the fossil species. There are occasional examples of *A. cervicapra* in which a vestige of an anterior keel exists, e.g. BM(NH) 27.2.14.41, 27.2.14.50 and 32.12.11.8, and this keel descends to a medial rather than to an antero-medial insertion, which is also like *P. rotundicornis*. Finally, although the horn cores of *P. rotundicornis* are neither so slender nor spiralled so closely to the central axis as in *A. cervicapra*, they are less massive than in the other fossils (Text-figs 11, 13, 14) and thus approach the living form more closely. These characters all make *P. rotundicornis* the best choice as the species to which *A. cervicapra* could be related. However the more important conclusion is that the group of *Prostrepsiceros* and *Protragelaphus* as a whole is related to the blackbuck and not to tragelaphines.

A. cervicapra differs from *Prostrepsiceros* by its very large supraorbital pits, smaller preorbital fossa, wide anterior tuberosities of the basioccipital (Text-fig. 15), and very large mastoid. Face and dental characters differing from *P. houtumschindleri* are the shorter and wider nasals, very small or absent ethmoidal fissure, more hypsodont teeth, occasional presence of indentations into the back edge of the rear central cavities on the upper molars, earlier fusion of the medial lobes of the upper molars, less backwardly inclined metaconid of P_4, and absent P_2. The percentage diagrams (Text-figs 14 and 15) show that *A. cervicapra* has supraorbital pits fairly wide apart, a relatively wide and low braincase, and a short premolar row. There is no reason to suppose that any of these characters are primitive and could preclude the blackbuck from descent from or relationship to the fossil genus. However they are probably sufficient to retain *Prostrepsiceros* as a separate genus from *Antilope*.

A. cervicapra differs rather more from the larger *Protragelaphus skouzesi*. Apart from characters in which it is advanced, it has a less low and wide skull, horn cores less massive at the base, no posterior keel on the horn cores and less open spiralling, horn cores not inserted so posteriorly, more strongly projecting orbital rims, braincase less angled on the face axis, frontals not hollowed, flatter nasals, the median indentation at the back of the palate passing forward of the lateral ones, palatine foramina close together, goat folds on the lower molars, and no paraconid-metaconid fusion on P_4. It can scarcely have descended from *P. skouzesi*.

A. cervicapra differs still more strongly from *Palaeoreas lindermayeri*, which accords with my conclusion that the latter can best be classified as a small ovibovine. The differences are less massive horn cores at the base, no deep irregular longitudinal grooving, horn cores less thick, no posterior keel nor a weak anterior one, some spiralling of the horn cores rather than a mere twisting of their axis, not such a deep post cornual groove, orbital rims strongly projecting, braincase not strongly angled, longer braincase, frontals low between the horn bases, no raising of the mid-frontals suture, infraorbital foramen high over P^3, a less strong median ridge on the occiput, poor styles and ribs on the upper molars, the lateral wall of P_4 indented in front of the hypoconid, P_3 relatively smaller, and the front and back edges of P_3 and P_4 not set transversely.

Phylogeny of spiral horned Antilopini

On the question of phylogeny, not a lot can be said, particularly in the absence of detailed time correlations of the sites where the varieties of horn core types occur. It is possible to conceive that the Maragha and Samos forms of *P. rotundicornis* are later than that in Pikermi, in so far as they are more gracile and therefore remote from *P. houtumschindleri*. However this conclusion is the more doubtful by the fact that the Pikermi form of *Sporadotragus* appears more advanced than at Samos. Bearing in mind the possibility of a time span at Samos, it is as well to follow the speculation no further. On the whole *P. rotundicornis* shows more signs of ancestry to *A. cervicapra* than any other of the Pliocene species, and it is a pity that it is less completely known than *P. houtumschindleri* or *Protragelaphus skouzesi.*

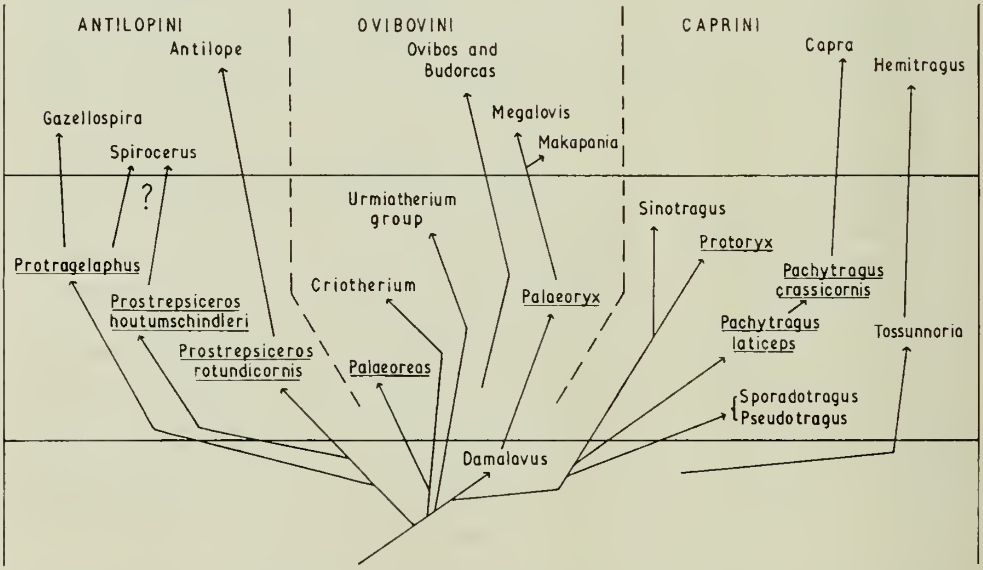

Fig. 16. Possible relationships of bovids mentioned in this paper. Names of species and genera which have been dealt with at length are underlined. The middle horizontal band contains forms known from Samos and other sites of broadly the same age. The upper band is for later forms, and the lower one is for a pre-Samos time level. Precise origins are not shown for *Spirocerus*, *Ovibos* and *Tossunnoria*.

It is certainly possible and very plausible to link *Protragelaphus skouzesi* with the similar European Villafranchian *Gazellospira torticornis* (Aymard), which Pilgrim & Schaub (1939) have already classified as an antilopine.

It would be interesting, were the material accessible, to assess the relationships of these European and West Asian spiral-horned antelopes with those of the Pliocene and Pleistocene of China. It is likely that there is a Pliocene species in China, *Antilospira licenti*, succeeded by the Pleistocene *Spirocerus wongi* (see Teilhard de Chardin & Piveteau (1930), Teilhard de Chardin & Young (1931), and Teilhard de Chardin & Trassaert (1938) for these Chinese antelopes, remembering that many of their specific names are likely to be synonyms. *Spirocerus wongi* dates from 1930, but is itself quite likely to be a synonym of the Russian *S. kiakhtensis* (Pavlow) 1910). It is tempting to see *S. wongi* as an eastern form of the same species or superspecies as *Gazellospira torticornis*, but *S. wongi* possesses an anterior keel and sometimes a weaker posterior one whereas *G. torticornis*, in common with the earlier *Protragelaphus skouzesi*, has a strong posterior keel and no anterior one. One wonders if *S. wongi* descends from the earlier *Antilospira licenti* and if that in its turn is related to *Prostrepsiceros houtumschindleri* or to *Protragelaphus skouzesi*, but I can write nothing useful about this.

A possible ancestor of the Pliocene spiral-horned antelopes is *Sivoreas eremita* (Pilgrim 1939 : 131, pl. 4 figs 1, 1a) from the Chinji stage of the Siwalik Hills (Gentry 1970 : 259). It has horn cores more medio-laterally compressed than in the lower Pliocene antelopes; anterior and posterior keels on the horn cores, the anterior one descending to an anterior rather than to an antero-medial or medial insertion; torsion of the horn cores and a narrow transverse ridge across the frontals between the horn bases. Much doubt surrounds the rather inadequate remains.

The living blackbuck is almost exclusively a grazer, and has some physiological adaptation to scarcity of water. In its undisturbed state it was an animal of flat plains and open woodlands, moving in big herds over areas of short grass. Its ecology was similar to that of a gazelle, although competition with *Gazella bennetti* was avoided. One can probably assume that *Prostrepsiceros* showed a tendency to inhabit the harsher environments, but this may not have applied to *Protragelaphus*.

The position of Palaeoreas lindermayeri

I had earlier written (Gentry 1968 : 874) that *Palaeoreas lindermayeri* should be placed in the Antilopini, along with *Prostrepsiceros* and *Protragelaphus*. However the comparisons on p. 273 have shown that it is very distinct from those Antilopini. I now think that although it is less phenetically remote from them than is any other ovibovine, there is a slight preference for assigning it to the Ovibovini because of characters it shares with the much larger *Criotherium argalioides*.

Besides the living muskox, *Ovibos moschatus* (Zimmermann), and takin, *Budorcas taxicolor* Hodgson, and their immediate Pleistocene relatives such as the fossil muskoxen of Europe, the early Chinese muskox *Boopsis sinensis* Teilhard de Chardin, and the early takin *Lyrocerus satan* Teilhard de Chardin & Trassaert, this tribe contains a number of other extinct genera and species. These are:

Urmiatherium polaki Rodler 1889 from Maragha,
Urmiatherium intermedium Schlosser 1903 from the Chinese lower Pliocene,
Plesiaddax depereti Schlosser 1903 from the Chinese lower Pliocene; (Bohlin (1935c) first assigned skulls to Schlosser's names for the last two species, which had been based on teeth),
Tsaidamotherium hedini Bohlin 1935a from the lower Pliocene of Tsaidam in western China,
Parurmiatherium rugosifrons Sickenberg 1933 from Samos,
Criotherium argalioides Major 1891a, 1892 from Samos.

In addition I have already referred the European Villafranchian *Megalovis latifrons* and its synonyms or relatives to the Ovibovini (see p. 282), and I also believe that the extinct *Makapania broomi* Wells & Cooke 1956 from the Transvaal is related to *Megalovis latifrons* (Gentry, in press). I shall not here enter into the complicated questions of a revision of this whole group. The Maragha and Chinese species of *Urmiatherium* appear to be very close to *Plesiaddax depereti* and the smaller *Parurmiatherium rugosifrons*, and all have specialized horn cores, a condition carried still further in *Tsaidamotherium*. All the Villafranchian and later ovibovines have a rather less extreme horn core morphology, and, as I have noted above, some of them may descend from *Palaeoryx pallasi*. *Criotherium*, known only from Samos, stands by itself with spiralled horn cores, but I am not ready to dispute Schlosser's (1904 : 27) and Bohlin's (1935b) opinions of its ovibovine affinities, chiefly because of dental similarities and its basioccipital morphology with strong paired longitudinal ridges and the trace of an enlargement of the posterior tuberosities. However it should be noted that the teeth of *Criotherium* are less advanced than those of *Urmiatherium* in retaining basal pillars on the lower molars, less rounded lateral lobes on the lower molars, and a longer premolar row. Also *Criotherium's* horn cores, fairly large preorbital fossa, fairly unenlarged occipital condyles, and basioccipital morphology are definitely less extremely specialized than in *Urmiatherium*. It is to *Criotherium* that I would now relate *Palaeoreas*.

It must be admitted that *Palaeoreas lindermayeri* differs from Ovibovini in many characters. It has its own specializations of a very deep postcornual groove, large supraorbital pits, and a long basioccipital. It also lacks quite a number of the specializations of later Ovibovini. It does not have a long face with anteriorly placed upper tooth row, the ethmoidal fissure is still present, the preorbital fossa is rather large, the infraorbital foramen is in a forward position instead of above P^3 or further back, the nasals are not parallel or almost parallel with the upper tooth row, the occipital condyles are not unusually massive nor are the posterior tuberosities of the basioccipital enlarged, the upper molars do not have rounded medial lobes, the lower molars do not have rounded and transversely narrow lateral lobes, they also do not have little outbowed medial walls or straight central cavities, and the cervical vertebrae lack enlarged centra. Some of these specializations, particularly those of the cervical vertebrae, condyles and basioccipital could be unnecessary in *P. lindermayeri* because of its smaller size.

In comparison with *Criotherium argalioides* the horn cores of *P. lindermayeri* are inserted less far behind the orbits, the braincase is longer and less angled on the face axis, basal pillars are slightly larger on its lower molars and sometimes present on its uppers, and there is sometimes a strong rib between parastyle and mesostyle on the upper molars. In all these characters the smaller form lacks the specializations of the larger, which is a frequent situation between related pairs of species of differing size.

In fact *Palaeoreas lindermayeri* can be regarded as a small and less specialized version of *Criotherium argalioides.* It shows the following strong agreements with that species:

The horn cores have a strong postero-lateral keel and a weaker anterior one.

There is deep irregular longitudinal grooving on some horn cores.

The axis of the horn cores is twisted, and twisted in the same direction as in *Criotherium*, and there is no open spiralling.

There is a localized raising of the mid-frontals suture forward of the horn bases and just behind the nasals. (This elevated suture is also to be seen in *Sporadotragus.*)

The central cavities of the upper molars remain joined to one another until fairly late in wear.

The left mandible BM(NH) M.15828 assigned to *Palaeoreas lindermayeri* has its P_3 and P_4 with transverse front and back edges (Pl. 6 fig. 2).

There is no valley in the lateral wall of P_4 in front of the hypoconid.

P_3 is fairly large in M.15828 in relation to P_4.

Some of the differences of *Palaeoreas lindermayeri* from all or various of the other spiral-horned antelopes considered in this paper also cause it to approach *Criotherium argalioides.* Such features are:

The rather massive horn cores of *Palaeoreas.* Their massiveness gives them an appearance of relative shortness.

The small divergence of the horn cores in anterior view.

The stronger angling of the braincase on the face axis.

The higher level of the frontals between the horn bases.

The usual disappearance of signs of the mid-frontals and parieto-frontals suture in adults.

The smaller separation of the supraorbital pits from one another.

A central longitudinal groove on the basioccipital.

The metaconid of P_4 not being directed backwards.

For these reasons it seems marginally better to place *Palaeoreas* in the Ovibovini than in the Antilopini, the resemblances to *Criotherium* being sufficiently strong to suggest not too remote a common ancestry. A count of skull character differences gave the result that *Palaeoreas lindermayeri* had 22 differences from *Protragelaphus skouzesi*, 15 from *Prostrepsiceros houtumschindleri* and 17 from *Criotherium argalioides*; this quantifies the problem and is an indication of how marginal the classification of *Palaeoreas lindermayeri* must be.

If it is accepted that *Palaeoreas* is an ovibovine, then it and *Criotherium* are the only members of the tribe with spiralled horn cores of any length. However this is probably not a severe isolating feature, because vestiges of spiralling remain in *Parurmiatherium*, and *Budorcas* and *Ovibos* have at least slight torsion. I don't think it would be advantageous to split them from other Ovibovini.

V. CONCLUSIONS

In a previous paper (Gentry 1970) I have described how the antelopes of the Fort Ternan upper Miocene site in Kenya, dated to 14 million years B.P., were closely related to Eurasian antelopes of the Vindobonian and equivalent time levels. They could be satisfactorily included in the tribes Boselaphini and Caprini, tribes which later became largely Eurasian in their distribution. It was just possible that some signs of ancestry to later African antelopes could be seen at Fort Ternan, but this was rather tentative, and the origin and development of African antelopes remains more undocumented than that of Eurasian ones. It is clear that some antelope groups confined to Africa by the historical period were also in northern India during the Quaternary and at least the later Tertiary. Work on such important African sites as Baringo, Kanapoi and Lothagam (Kenya) and Langebaanweg (Cape Province, South Africa) may throw more light on the history of African antelopes. This present paper on Samos has been intended to remove one source for confusion in deciphering this history. *Palaeoryx*, *Protoryx* and *Pachytragus* are not hippotragines and *Prostrepsiceros* and *Palaeoreas* are not tragelaphines. The only Samos antelope which at present looks as if it could be even remotely connected with the ancestry of any later African form is the unique skull of *Tragoreas oryxoides* (see above p. 284). In fact there are no firm grounds for detecting any African affinities among the Samos antelopes. They are more properly seen as an earlier stage in the evolution of Eurasian bovid faunas, and date from a time younger than the Fort Ternan fauna when regional differentiation must have been becoming more marked. I have discussed the historical zoogeography of antelopes at greater length in my Fort Ternan paper (Gentry 1970 : 310–317).

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VII. SUMMARY

This paper considers the classification, phylogeny and aspects of the zoogeography of two groups of antelopes prominent in the lower Pliocene fauna of Samos, and also known from the rich sites of Pikermi in Greece and Maragha in Iran.

Antelopes hitherto referred to a number of species of *Palaeoryx, Protoryx* and *Pachytragus* can be arranged in the following species:

Palaeoryx pallasi (Wagner) from Samos and Pikermi,
Protoryx carolinae Major from Pikermi,
Pachytragus laticeps (Andree) from Samos and Maragha,
Pachytragus crassicornis Schlosser from Samos.

Both *Pachytragus* species, and particularly the more advanced *P. crassicornis*, have affinities with the living goats (Caprini, *Capra*). *Protoryx carolinae* and *Palaeoryx pallasi* are related to *Pachytragus*, and none of these species belong to the African tribe Hippotragini, which is where they have been placed in Simpson's (1945) and other classifications of mammals, following work in the years between the two World Wars. *Protoryx carolinae* can be linked with Chinese lower Pliocene fossils and tentatively placed in the Caprini, while *Palaeoryx pallasi* could well be related to the Villafranchian ovibovine *Megalovis latifrons.* I suggest that *Palaeoryx* itself be placed in the Ovibovini.

Spiral-horned antelopes with anticlockwise torsion on the right side can be arranged in four species:

Prostrepsiceros houtumschindleri (Rodler & Weithofer) from Maragha and Samos,
Prostrepsiceros rotundicornis (Weithofer) from all three sites,
Protragelaphus skouzesi Dames from all three sites,
Palaeoreas lindermayeri (Wagner) from Pikermi and Samos.

Prostrepsiceros and *Protragelaphus* can both be taken as Antilopini, and are related more or less closely to the Indian blackbuck, *Antilope cervicapra. Palaeoreas lindermayeri* is best classified as a small and primitive ovibovine related to *Criotherium argalioides* of the Samos fauna. None of the spiral-horned antelopes from Pikermi, Samos or Maragha can be placed in the African tribe Tragelaphini. Bovids from these three sites can be seen as a stage in the evolution of those occurring later in Eurasia, and show no signs of relationship with African antelopes.

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